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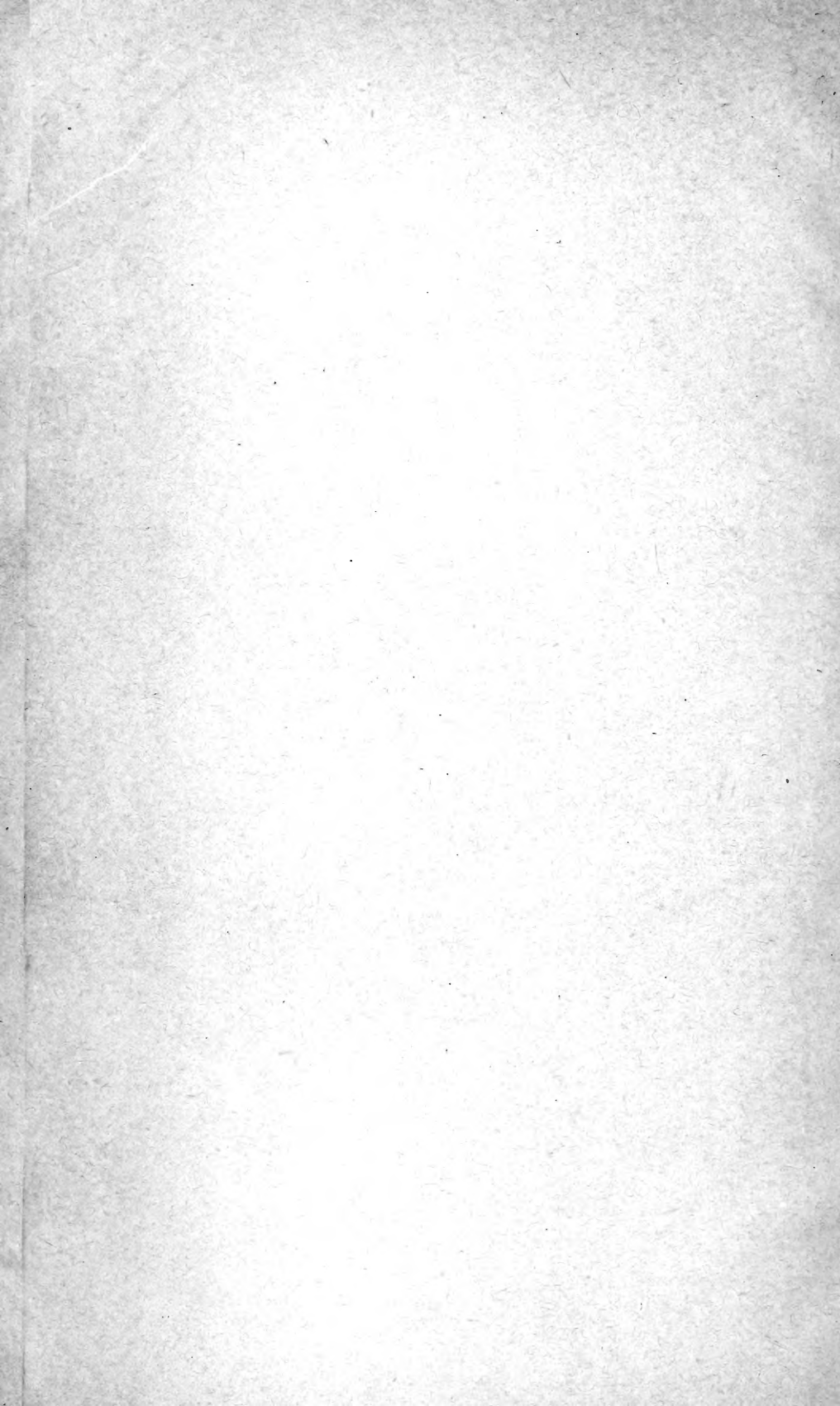
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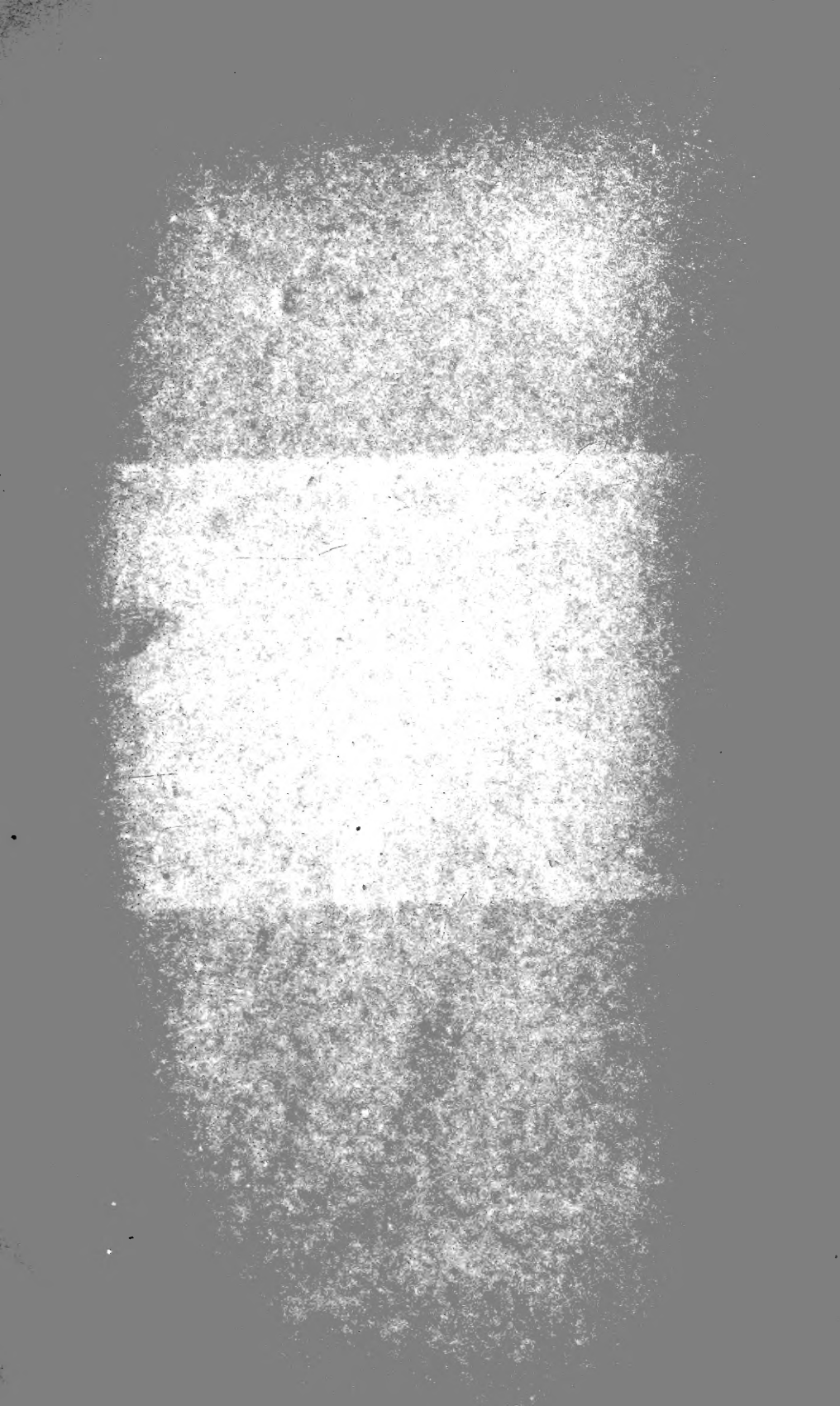
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THE JOURNAL
OF
Comparative Neurology

A QUARTERLY PERIODICAL DEVOTED TO THE
Comparative Study of the Nervous System.

EDITED BY
C. L. HERRICK, ALBUQUERQUE, NEW MEXICO.

ASSOCIATED WITH
OLIVER S. STRONG, COLUMBIA UNIVERSITY,
C. JUDSON HERRICK, DENISON UNIVERSITY.

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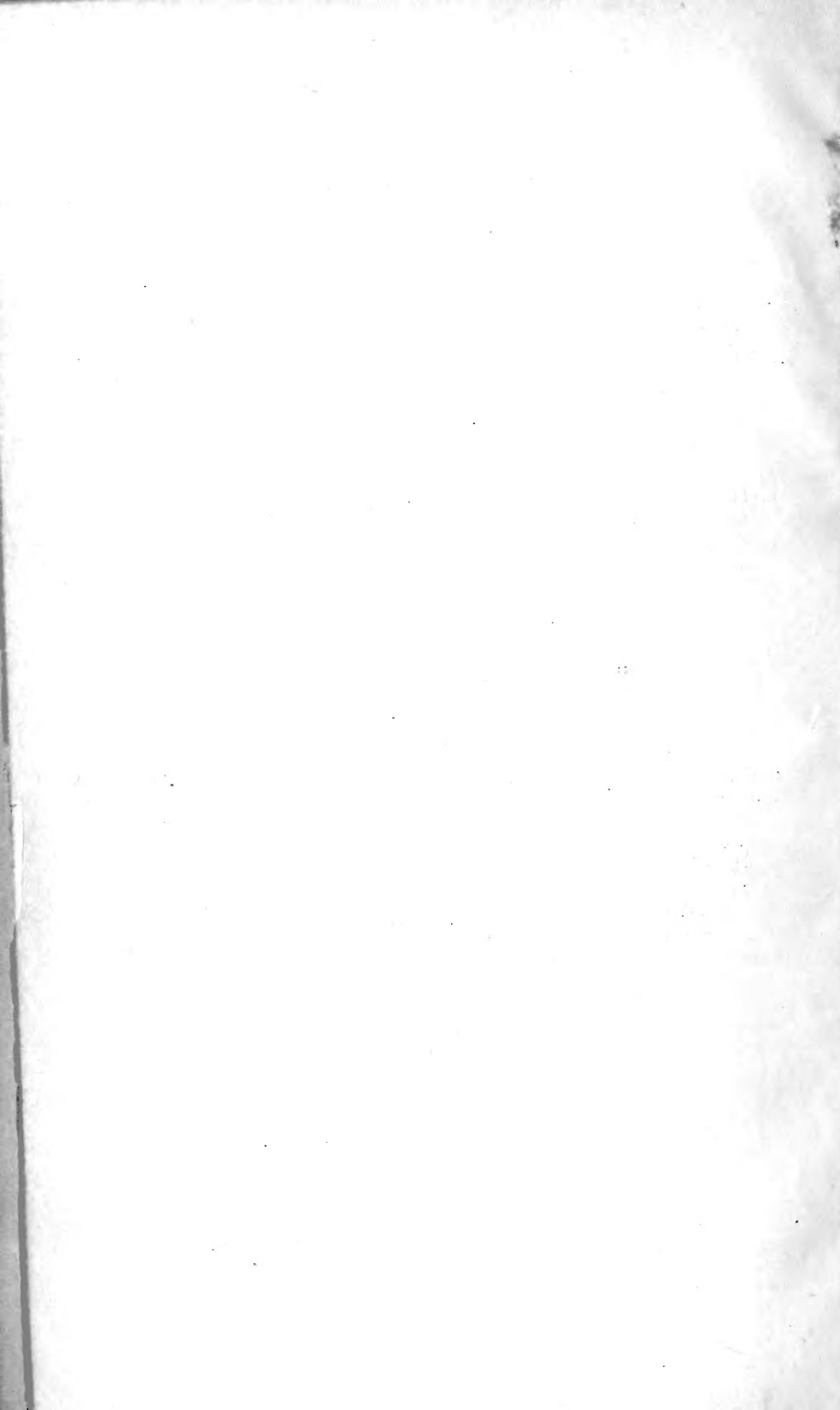
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VOLUME XII, 1902.

PUBLISHED FOR THE EDITORS BY C. JUDSON HERRICK,

GRANVILLE, OHIO, U. S. A.

R. Friedländer & Son, Berlin, European Agents.



THE JOURNAL OF COMPARATIVE NEUROLOGY.

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THE

JOURNAL OF COMPARATIVE NEUROLOGY.

THE BRAIN OF PETROMYZON.

By J. B. JOHNSTON,

Professor of Biology, West Virginia University.

With Plates I—VIII.

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I. INTRODUCTION.

The species used for this investigation is the common brook lamprey, *Lampetra wilderi*. GOLGI preparations were made in 1897 and others in 1898 for the purpose of making some comparisons with the brain of *Acipenser*. So many points of interest were noted that it was decided to lay the preparations aside for more complete study later. The paper deals with the minute structure of the various brain centers, the fiber tracts and the central relations of the cranial nerves. It is a contribution to our knowledge of the mechanism of sentient life in lower vertebrates, as a foundation for the study of the localization of central nervous functions and the physiological (psychological) significance of the various regions of the higher vertebrate brain. An attempt has been made in the study of the brain of the sturgeon and of the lamprey to seek out the earliest or most primitive form of the well known brain centers of higher forms, to study them with reference to their possible

origin from still more simple and generalized structures, and to compare or connect them with the parts of the spinal cord. In all parts of the brain this attempt has resulted in the discovery of more primitive conditions than have hitherto been known, and it has been possible to trace the probable course of growth and differentiation in certain brain centers from lower to higher vertebrates. The chief significance of the present paper lies in the fact that by the study of a lower vertebrate than the sturgeon it carries this investigation to a fuller knowledge of facts and to more certain conclusions.

As in the study of the sturgeon brain, the work has been done by means of GOLGI sections with the aid of haematoxylin preparations and dissections. The GOLGI series were obtained by treating the whole heads by the rapid osmium-bichromate method and cutting complete series in the three conventional planes. In some cases the ventral half of the head was cut away before hardening, but in all cases the ganglia of the cranial nerves and (all or a sufficient part of) the peripheral course of the nerves was intact and impregnated so that the principal nerve rami could be identified with certainty. The haematoxylin sections were also used in analyzing the roots and ganglia and, although there are some points of extreme difficulty owing to the small size of some of the nerve roots, it is thought that in the light of the recent work of STRONG, COLE, HERRICK and JOHNSTON both the central relations and the peripheral distribution have been correctly made out. No attempt has been made to work out the distribution in detail, and the description of the sense organs and cranial nerves is given a subordinate position as an introduction to the discussion of theoretical questions concerning the sensory centers of the medulla.

It gives me pleasure to acknowledge my indebtedness to Professor S. H. GAGE of Cornell University and Professor J. E. REIGHARD of the University of Michigan for hardened material sent me during the past year. Through the courtesy of the officials of the Marine Biological Laboratory at Woods Hole I have been enabled to complete the work while occupying a room for research in the laboratory during the past summer.

After the manuscript was completed and about to be sent to the printer the excellent paper of HOUSER on the neurones of the selachian brain came into my hands. I have added brief comments upon such parts of this paper as touch upon matters treated in the present paper. It is unfortunate that Professor HOUSER has not treated of the fiber tracts, and has given neither general figures nor a description of the nerve roots by which to identify the sensory centers in the medulla.

II. GENERAL DESCRIPTION.

The gross internal anatomy of the brain as it may be made out from a series of cross sections is given here in order to make clear the description of the minute structure which follows. The external form is shown in Fig. 1, and the figures in WIEDERSHEIM's textbook will apply to the brain of *Lampetra*, with the exception of the nerve roots. There seems to be a great difference in curvature in different individuals. Compare Figures 1 and 2, both of which are from brains hardened *in situ*. This has made it difficult to bring general sketches like that in Fig. 30 into agreement with transverse sections. No attempt has been made to do this.

The dorso-ventral flattening of the spinal cord and the corresponding form of the grey matter have been described by several authors. (Cf. KÖLLIKER, '96, Fig. 425). In the grey matter large cells are found in two places. Just dorsal to the central cavity are the dorsal or giant cells arranged somewhat irregularly in pairs. At either lateral extremity of grey matter are the motor cells. The remainder of the grey is made up of smaller cells which include the cells corresponding to the dorsal horns of other vertebrates, and the tract and commissural cells. In the white matter there are a large number of very thick fibers, the MÜLLERIAN fibers. About eight of these form a median ventral group beneath the grey matter on either side, while many others of varying thickness are scattered in the lateral and dorso-lateral parts of the white matter. The median dorsal part of the white matter, bounded laterally by the dorsal

roots of the spinal nerves, is entirely free from these thick fibers. This area may be divided into two portions which are quite distinct in the region of the first three spinal nerves: a lateral portion which is made up of somewhat coarser and more deeply staining fibers, and a median portion whose fibers are very uniform in diameter, finer than those of the lateral portion, and take a pale stain in iron haematoxylin. The lateral, deeply staining area receives the fibers of the dorsal roots, the median pale portion seems to be continuous cephalad with the fasciculus communis center only.

The transition from the cord to the medulla is marked by the following changes (Figs. 3-7). The cord becomes compressed or contracts laterally until it first assumes a round form and then becomes thicker dorso-ventrally than from side to side. At the same time the central canal becomes larger and oval in outline, rises slightly toward the dorsal surface, then becomes wider near the dorsal surface and finally opens out into the wide ventricle with choroid roof. As the cord assumes the cylindrical form the large cells in the lateral part of the grey gradually approach the ventral raphé until they take up the characteristic position of ventral horns and by this movement the median group of MÜLLERIAN fibers are crowded into a compact bundle between the ventral horns and the raphé. At the same time that portion of the grey which lies, lateral to the canal in the cord becomes greatly increased and thickened dorso-ventrally, the dorsal or giant cells disappear, and the thickened grey mass extends up at the sides of the enlarged canal and becomes continuous with the nucleus of the dorsal funiculi. This latter appears in line with the lateral, deeply staining portion of the dorsal white matter described above. The difference in the staining properties of these two areas seems to disappear as the medulla is approached but the median area remains free from cells except in the immediate neighborhood of the central canal, and just before the canal opens out into the fourth ventricle the median areas of the two sides are connected by a commissure over the ventricle. This is the commissura infima HALLERI, and marks the tracts in question as

the cervical bundles of CAJAL which continue the fasciculus communis system into the cord.

The great increase of the grey matter dorsally results in an apparent or relative crowding ventrad of the lateral and ventral tracts, and the medulla of *Petromyzon* in front of the calamus scriptorius assumes the appearance of an entirely characteristic fish medulla. The most dorsal and median portion of each lateral wall is occupied by the fasciculus communis center (lobus vagi). Latero-ventral to this is the nucleus funiculi, or, farther forward, the tuberculum acusticum with the spinal V tract bounding it ventrally. Ventral to this are the lateral and ventral tracts with the central grey matter adjoining the cavity. In this there are two distinct columns of motor cells, one lateral and one ventral in position. In the region of the calamus the large hypoglossus nerve takes its origin from the ventral group of motor cells by several rootlets which are surrounded by the cells of the lower olive. The sensory and motor roots of the IX and X nerves take their apparent or external origin high up on the lateral surface of the medulla, at about the level of the spinal V tract, as will be described more fully below.

Passing forward, the acusticum grows larger and by the time the level of the VII and VIII nerves is reached the fasciculus communis has lost its dorsal position and has become a small bundle of fine fibers recognizable with difficulty between the acusticum and the central cavity (Figs. 10, 11). At the same time the lateral group of motor cells has grown extremely large and projects into the cavity as a great rounded ridge which extends from just behind the root of VII to the point of exit of the sensory V. The fasciculus communis disappears from sections in front of the VII root, the spinal V tract rises to a more and more dorsal position, and finally emerges from the dorso-lateral surface of the medulla at its extreme cephalic end as the sensory root of V (Figs. 1, 12, 13). Somewhat further caudally the large lateral column of motor cells gives rise to the very large motor root of V, and immediately in front of this to AHLBORN's VI, and then quickly disappears from sections.

In the mean time the acustica of the two sides arch over the ventricle toward one another and fuse to form a bridge of tissue scarcely as thick as the acustica themselves, the cerebellum (Fig. 12). In the cerebellum are recognizable the characteristic granular and molecular layers, although they are poorly differentiated.

Above the cerebellum there appears the bilobed tectum opticum (Figs. 12, 13), which presents an appearance in transverse section very closely resembling that of the tectum of *Acipenser* in the form of the cavity, the arrangement of the white and grey matter, and in the dorsal decussation. A little farther forward the dorsal decussation disappears and the median part of the roof of the mid-brain becomes a choroid plexus (Fig. 14). Conspicuous in the base of the mid-brain are the III nerve with its nucleus and decussation, and the decussation of the bundles of MEYNERT (Fig. 24). In the cephalic part of the mid-brain the tectum has receded far to the sides, leaving the whole dorsal wall to be made up of the choroid plexus (Fig. 14), and the transverse section of the nervous tissue has nearly a simple U-form. In the lateral wall appear the bundles of MEYNERT, the right one being several times larger than the left. Farther forward the dorsal edges of the lateral walls become connected by the large posterior commissure (Fig. 15).

Beneath the base of the mid-brain appears in section the most caudal portion of the 'tween-brain, the corpus mammillare. It has a thick nervous caudal wall and a thin ventral wall which constitutes part of the saccus vasculosus. The cavity of the corpus mammillare enlarges and opens into the 'tween-brain ventricle in about the same transverse sections in which the posterior commissure comes to be replaced by the ganglia habenulae and the superior commissure. The right ganglion habenulae is very much larger than the left (Fig. 16), the difference in size being much greater than in *Acipenser*. Immediately in front of the posterior commissure and behind the superior commissure a small irregular diverticulum of the third ventricle gives rise to the very attenuated stalk of the epiphysis (Fig. 2). This extends forward a little to the left of the middle

line and expands into the epiphysis dorsal to the fore brain. In the choroid roof of the 'tween- and fore-brain, immediately ventral to the stalk of the epiphysis, there extends forward from the left ganglion habenulae a bundle of fibers which expands into a grey mass beneath the epiphysis. This is the *Zirbelposter* of AHLBORN ('83).

Looking again at the ventral portion of the 'tween-brain, it is seen that in transverse sections in the plane of the superior commissure the lateral walls fuse together in such a way as to close off the ventral part of the cavity from the third ventricle. This part of the cavity of the inferior lobes is triangular in transverse section and extends forward to the optic chiasma beneath the caudal border of which it ends blindly, forming thus a very deep postoptic recess (Fig. 19). The tissue which roofs over this recess contains the large postoptic decussation, in front of which the optic tracts decussate before leaving the brain.

In sections through the optic chiasma no other part of the 'tween-brain is present, but instead the sections pass through the body of the fore-brain. The lateral lobes, or so-called hemispheres, of the fore-brain are seen at the sides of the 'tween-brain in sections considerably caudal to the chiasma (Figs. 18, 19). In sections just in front of the chiasma the rounded cavities of these lobes communicate widely with the central cavity. Below this point of communication the lateral walls constitute the corpora striata in the narrow sense, between which the cavity is produced ventrally into a characteristic pre-optic recess surrounded by the substance of the nucleus thæniæ. Above the lateral expansions of the cavity appears on either side a prominent ridge which forms the dorsal part of the lateral wall of the fore-brain from a point a little in front of the ganglia habenulae to the olfactory commissure (Figs. 17, 18). This is the *epistaiatum* (optic thalamus and striatum of AHLBORN, thalamus (?) of FRIEDRICH MAYER, '97). The lateral lobes above mentioned are divided externally by a slight groove into anterior and posterior parts (Fig. 1), and internally the lateral expansions of the cavity divide into anterior and poste-

rior horns. The posterior part (hemispheres of AHLBORN) corresponds to the olfactory area of other fishes. The anterior part is the olfactory lobe. The periphery of the olfactory lobe contains glomeruli which appear larger and better defined than in most fishes.

The floor of the fore brain ventricle contains the small anterior commissure just in front of the preoptic recess and is thin from that point forward, constituting the lamina terminalis. At the dorso-cephalic border of this lamina is the olfactory commissure.

III. MINUTE ANATOMY.

It is not my purpose in what follows to give a full and detailed account of all parts of the brain for purposes of description merely. Since this detailed account has been given for the brain of *Acipenser* the mere description is of little value except where it is necessary in order to distinguish certain nuclei or centers or to set forth accurately the functional connections between various parts of the brain. I shall therefore omit all detailed description of structures which closely resemble the corresponding structures in *Acipenser*, or which present no peculiarities of general significance.

A. *Hind Brain.*

a. Motor nuclei and motor nerve roots (Figs. 6-13).

The existence of two distinct motor columns in the medulla has been mentioned above. The ventral column lies at either side of the ventral groove of the ventricle and is a direct continuation of the ventral horn of the cord. The lateral column makes its appearance slightly caudal to the calamus and extends forward just ventral to the lateral groove or angle of the ventricle. In the caudal part of the medulla, i. e., nearly up to the root of VIII, neither column makes any appreciable projection or ridge in the cavity. There is no mingling or interlocking of the cells of the two columns, but there is everywhere a considerable space between them. In front of IX both columns grow smaller and practically disappear for some distance

between IX and VIII. Both reappear just behind the root of VIII; the ventral continues for about one-half millimeter in the region of the VII-VIII root complex (Fig. 11), and the lateral continues forward to the root of VI at the isthmus. This cephalic part of the lateral column forms a large projection into the ventricle.

The cells in both columns are usually spindle-shaped, closely set, and the dendrites have long branches spreading widely in the fiber tracts. The cells in the cephalic part of the lateral column are so numerous that they are crowded into a radial arrangement (Fig. 11 a). The cell bodies are much elongated and distinctly spindle-shaped; they converge toward the outer part of the column, which lies near the spinal V tract, and diverge toward its internal convex border. The inner ends of the cells give off many small dendrites which form a fiber zone of considerable thickness between the motor cells and the ependyma. Larger dendrites from the outer ends of the cells penetrate the lateral tracts. The spaces between the cell bodies seem to be entirely free from fibers.

The mode of origin of the motor nerve roots is as follows. The large hypoglossus arises by several rootlets in cephalocaudal succession, the fibers coming from the cells of the ventral motor column of the same side (Fig. 6).

The roots of X, both sensory and motor, are so small that it is impossible to make out their central relations without the aid of GOLGI sections. The motor roots can be traced in haematoxylin sections and it is apparently these which AHLBORN ('84) has described under the name of the "vier hinteren sensiblen Vaguswurzeln." The root described by him as the motor vagus is a part of the hypoglossus. The "vier hinteren sensiblen Vaguswurzeln" arise according to AHLBORN from the "obere laterale Ganglion" of LANGERHANS, i. e., from the group of cells described above as the lateral motor column. Four such rootlets are found in *Lampetra* and, as GOLGI sections show, at their point of exit from the medulla they contain both sensory and motor fibers intricately interwoven. The sensory fibers run on to the dorsal median portion of the medulla (Fig. 8). They

can not be traced to their endings in haematoxylin sections and consequently AHLBORN has mistaken for them the motor roots which arise from the lateral column of large cells.

The motor root of IX is not mingled with its sensory root, but lies considerably ventrad and cephalad from it, nearly in the same transverse section as the postauditory lateral line root (*l. l. X*, Figs. 1, 9, 10). It is larger than the motor roots of X.

The fibers of the motor VII arise from the cells of the lateral motor column in the caudal part of its cephalic half (Fig. 11). The fibers are fine and collect into two bundles as they leave the motor column; one bundle pierces the ventral part of the spinal V tract, the other the dorsal part. The bundles are not traceable as such through this tract, but are broken into small, fasciculi or single fibers. The fineness of the fibers makes it difficult to distinguish them from the fasciculus communis fibers of VII, with which indeed they seem to be mingled as they emerge from the medulla. In the absence of a knee bend in the root of the motor VII, *Petromyzon* seems to differ from all other vertebrates.

As AHLBORN states, the motor V receives fibers from two sources (Figs. 11, 12, 13). The main portion of the cephalic half of the lateral motor column is the place of origin of the greater part of the large root. A small part of the fibers form what AHLBORN called the ascending root of the motor V. He traced these fibers caudally in the medulla but could not find their place of origin. I find that they come from the isolated cephalic portion of the ventral motor column which lies at the level of the VII-VIII root complex.

I am unable to verify AHLBORN's account of the VI nerve. A root of considerable size arises from the cephalic end of the lateral motor column (Fig. 13), runs independently for some distance, and joins the motor V root as the latter enters the Gasserian ganglion. Thus far AHLBORN's account is clearly correct. Beyond this point I am unable to trace the bundle with certainty, but it seems to become permanently united with the V trunk. I am inclined to the opinion that the root in question belongs to the V and that the VI is to be looked for else-

where. This conclusion is supported by the following considerations. The root is larger than the condition of the eyes would lead us to expect. The nucleus from which it arises is universally devoted to visceromotor nerves, while VI is somatic. Finally, this root is lateral while the VI root is ventral in all other forms. The only suggestion which the writer can make is that the equivalent of VI is found in the bundle of coarse fibers in V which arise from the ventral motor column in the region of VII and VIII. This isolated portion of the ventral motor column occupies the same position as the nucleus of VI in *Acipenser*. I hope to reinvestigate this interesting point on more suitable preparations.

I have been unable to trace the IV nerve to its cells of origin. It is very small (Fig. 13).

As described by AHLBORN, the nucleus of III is in two parts (Fig. 34). The roots decussate beneath the aqueduct but not all the fibers cross. One portion of the nucleus of origin lies at either side of the median line beneath the aqueduct and most or all of the fibers arising from it decussate. This is a compact mass of cells lying rostral to the root bundles, while immediately caudal to the roots a similar mass of cells constitutes the end-nucleus of the bundles of MEYNERT. The other portion of the nucleus consists of larger, spindle-shaped cells which lie close around the root at its exit, the greater number of cells being massed on the cephalic surface of the root. Some of the cells project beyond the general contour of the brain with the issuing root. The fibers of these cells are said by AHLBORN to cross to the opposite side, with few exceptions. The opposite is the case, since many fibers are readily traced into the nerve of the same side while I have been unable to trace any to the opposite side.

b. The Müllerian fibers.

AHLBORN has described the MÜLLERIAN fibers in three bundles, a lateral uncrossed, a median crossed, and a median uncrossed. The lateral uncrossed and median crossed bundles arise from the spindle cells situated among the fibers of the VIII roots. Each of these cells sends a peripheral process out

in the lower VIII roots while a central process becomes a MÜLLERIAN fiber. There is a very conspicuous decussation or chiasma of these fibers a short distance caudad from VIII. These spindle cells and the coarse central processes coming from them exist in the acusticum and will be described below in connection with that center. These structures, however, have nothing to do with the MÜLLERIAN fibers. The proof of this is that the cells in question are much more numerous than the MÜLLERIAN fibers, that other cells of exactly the same character exist in the cephalic part of the acusticum and send their fibers cephalad to cross in the ansulate commissure, and that the MÜLLERIAN fibers do not decussate.

The fibers can be traced with ease to certain large cells situated among the motor cells. The relative size of these and the motor cells is shown with approximate accuracy in Fig. 11 a. I have counted these cells in a single haematoxylin series and find them distributed as follows: in the caudal half of the ventral motor column, 10; in the cephalic half, on the left side 7, on the right side 6; in the immediate vicinity of the V root, 1 pair; in the vicinity of the IV root, 1 pair; in the vicinity of the III root 1 pair; a little farther forward and dorsad, 1 pair; a little farther forward and ventrally, 1 pair. These large cells are like motor cells in lying near the cavity and sending large dendrites among the fiber tracts, and they closely resemble the large cells in *Acipenser* from which the MAUTHNER'S fibers arise. A pair of cells much larger than the others, which lie in the lateral motor column at the level of VII are possibly directly homologous with MAUTHNER'S cells in *Acipenser* (Fig. 11 a). At the caudal end of the medulla there are about forty fibers large enough to be conspicuous and of these from twenty to twenty-four are very much larger than the rest. These probably arise from the very large cells, while the smaller fibers arise from cells not easily distinguishable from the motor cells.

AHLBORN thinks, indeed, that his median uncrossed fibers arise from the large cells here described, but he is in doubt whether the fibers which he has seen are in reality MÜLLERIAN

fibers. F. MAYER ('97) has mentioned the three pairs of cells in the vicinity of III as giving origin to MÜLLERIAN fibers.

c. General and special cutaneous centers (somatic).

These centers include the nucleus funiculi, the nucleus trigemini spinalis, the tuberculum acusticum, and the cerebellum. It will be necessary to give a somewhat more complete topographical description of these centers and of the nerve roots than was given in the general account above.

As the cord passes into the medulla there is a very great thickening of the grey matter just lateral to the central canal and gradually cells spread through the dorsal tracts, forming a diffuse nucleus funiculi (Fig. 9). None of these cells invade the most median part of the dorsal tracts which belongs to the fasciculus communis system. Farther forward the region of the dorsal tracts and nucleus funiculi becomes transformed into three distinct structures. There appears first in the peripheral part of the nucleus and parallel with the surface of the medulla, a thin crescent-shaped plate or lamina of cells (Fig. 9), which are evidently derived from the nucleus funiculi but gradually become distinct from it. The body of the nucleus is continued forward by a large tract of fibers, the spinal V. Throughout its whole extent the spinal V has cells scattered among its fibers so that it retains the appearance of the nucleus funiculi, although the cells are not so numerous (Fig. 11 a). At the same time that the nucleus funiculi merges into the spinal V tract the plate of cells becomes divided into two distinct nuclei (Fig. 9 a). One of these lies directly dorso-lateral to the spinal V and accompanies this tract throughout nearly its whole extent. In its caudal part it is a compact nucleus with a light space about it. Although its cells decrease in number and become less easily distinguished from the nucleus above it as it passes forward, it is recognized as a light space directly overlying the spinal V and separating it from the VII and VIII roots, and is finally replaced by the collection of spindle cells to be described below. I shall call this the nucleus of the spinal V.

The other nucleus developed from the common lamina of cells lies just dorsal to the last and in its caudal part appears

more dense and much more deeply stained. It is the tuberculum acusticum. Its deep stain is due to the density and complexity of the fiber endings in it. It appears first as a small deeply staining mass which soon grows larger and occupies the outer half of the extreme dorsal part of the medulla wall, the inner half being occupied by the lobus vagi (fasciculus communis, Fig. 9 a). At about the level of IX the acusticum comes to overtop the lobus vagi which continues forward as a fasciculus between the acusticum and the fourth ventricle (Fig. 10). The acusticum becomes the largest grey mass in the medulla at the level of the VII-VIII root complex and contains three more or less distinct nuclei (Fig. 11 a). A short distance cephalad from IX there are recognized two groups of cells which occupy ventrolateral and dorso-median positions in the acusticum. The dorsal group receives the root of the lateral line X nerve. The ventral group contains somewhat farther forward the spindle cells from which AHLBORN derived the MÜLLERIAN fibers, and the greater part of the VII-VIII roots enter through this group. Dorsal to both these nuclei, and partially separated from them by an area of fine fibers, is another group of cells which receives the larger part of the lateral line VII nerve. Farther cephalad this most dorsal of the three nuclei wholly disappears. The dorsal one of the other two gradually takes a more median position while the ventral one lies lateral to it. The area of fine fibers which separates these from the third now forms a distinct fine fibered layer on the dorso-lateral surface of these two nuclei. The median nuclei of the two sides now approach one another and at the same time the median and lateral nuclei become almost indistinguishable. In this manner they both enter into the formation of the granular layer of the cerebellum, while the fine fibered layer forms the molecular layer.

From this description it appears :

1. That there is a special, although diffuse, nucleus funiculi at the junction of the cord and medulla.
2. That this nucleus is in direct continuity with both the nucleus of the spinal V and the tuberculum acusticum.
3. That the acusticum is in direct continuity cephalad

with the granular layer of the cerebellum and that there is a well-defined prolongation of the molecular layer backward over the acusticum. This is homologous with the cerebellar crest of *Acipenser* and selachians.

4. That there is a distinct nucleus lying dorsal to the acusticum proper and partly separated from it by the cerebellar crest, which receives the fibers of part of the lateral line VII nerve. This nucleus is homologous with the lobus lineae lateralis (so-called lobus trigemini) of *Acipenser* and selachians.

A careful examination of the elements of these several nuclei and of the mode of ending of the sensory fibers in them throws additional light on their relationship and their probable history.

1. Nucleus funiculi (Figs. 6-9, *d. h.* and *n. f.*).

The spinal V tract enters the nucleus at its ventral border and the fibers take a dorso-caudal course, so that they are cut very obliquely in transverse sections. In the middle and cephalic part of the nucleus these fibers form a dense mass, being more closely packed at the ventral angle, and between them the cells lie scattered without any regular arrangement. The character of the cells may be seen from the figures. The greater number are large cells ($10-24 \times 16-50 \mu$) of various forms whose dendrites are large and well branched. Their neurites go as internal arcuate fibers across the ventral raphé. The small cells ($8-10 \times 10-14 \mu$), are few in number and have short, poorly branched dendrites. I have been unable to trace the neurites of these cells to my satisfaction.

2. Nucleus trigemini spinalis.

The nucleus accompanying the spinal V tract is never clearly impregnated in my preparations. When the cells are impregnated there is so much precipitate between them that it is impossible to give an accurate description of the larger cells. They have the same appearance in haematoxylin sections as those of the nucleus funiculi. In a few cases smaller cells ($8-10 \times 10-12 \mu$) were found, and these closely resemble the smaller cells of the nucleus funiculi and acusticum.

3. Tuberculum acusticum (Figs. 10, 11).

In GOLGI preparations it is difficult or impossible to distinguish between the caudal part of the acusticum and the nucleus of the spinal V and the nucleus funiculi. For this reason the following description of the acusticum is taken from that part in front of the lateral line X root. In this part of the acusticum there are three kinds of cells: large and small cells resembling those of the nucleus funiculi, and a peculiar type of spindle shaped cells. The first two are found in all three acusticum nuclei, the third only in the lateral nucleus. The large cells are found in part among the fiber bundles and in part adjoining the ventricle, with a central process among the ependyma cells. They vary greatly in both size ($8-16 \times 14-48 \mu$) and form, many of them vividly recalling the large irregular cells in the acusticum of *Acipenser*. The neurites of these cells go as arcuate fibers across the ventral raphe.

The small cells do not appear to be very numerous, but this is probably due in part to their failure to become impregnated. They measure $8-9 \times 8-16 \mu$, and are always sharply distinguished from the large cells by the facts that the cell bodies are compact (rounded) and lie among the fiber bundles, never adjoining the ventricle, and that the dendrites are short and poorly branched. The neurites could not be traced far from the cells.

The spindle cells are seldom impregnated in GOLGI preparations, but in iron haematoxylin sections they are clearly differentiated by their simple form and by their sharp deep black stain. Their position is indicated in Figs. 11, 11 a, 12; their structure is shown in Fig. 23. As noted above, AHLBORN described these cells as having central processes which become MÜLLERIAN fibers and peripheral processes which go out in the VIII nerve. It has been shown above that the MÜLLERIAN fibers are not processes of these cells and it will be shown here that the VIII fibers do not arise from them. In iron haematoxylin sections certain coarse fibers of VIII and the lateral line VII have a direct course and take the same deep stain as do the spindle cells and their processes. These sharply stained fibers pass in part forward and in part backward in the lateral

nucleus and seem at first sight to be continuous with the outer ends of the spindle cells which are distributed throughout almost the whole extent of this nucleus. On closer examination every favorably placed cell appears to have a more deeply stained area at the outer end. This area proves to be not a part of the cell but an enlarged ending of the sensory fiber. This ending is shaped like the bowl of a spoon and overlaps about one-fourth or one-third of the cell from the outer end. In AHLBORN'S figure ('83, Fig. 49) there appears a light area at one end of the cell, which probably indicates that in his borax carmine preparations the fiber endings failed to take the stain.

The cells are quite uniform in size and shape. They measure about $8 \times 32 \mu$, and the club-shaped ending of the fiber is about $7 \times 12-14 \mu$. The cells are almost perfect spindles and probably regularly bear processes at each end. The peripheral process is sometimes made out in iron haematoxylin sections and in one case where the cell was impregnated with silver there was a good sized dendrite running nearly parallel with the sensory fiber. From the inner end of the cell arises a neurite of medium thickness which grows larger farther from the cell. All these neurites go ventro-mesad and cross in the ventral raphé. Two conspicuous decussations are formed by bundles of these fibers, while many run singly and do not attract attention. One of the decussations lies a little caudal to the VIII root and was called by AHLBORN the chiasma of the MÜLLERIAN fibers (Fig. 10). The other decussation is formed by fibers coming from cells lying in the extreme anterior end of the lateral acusticum nucleus. The fibers pass forward and downward and cross in the ansulate commissure close to the decussation of the III nerve (Figs. 2, 24). All these neurites have in all essential respects the relations of internal arcuate fibers and I believe they are to be classed as such. The whole spindle cell apparatus probably does not exist above the Cyclostomes.

In GOLGI sections there appear many club-like endings of lateral line fibers in the acusticum. It is probable that these are the fibers just described, the cells not being impregnated.

The disposition and ending of the sensory roots in the

acusticum may be described best by beginning with VIII (Figs. 1, 11, 11 a, 12, 29, 30). In transverse sections the VII-VIII root complex is the most conspicuous of the nerve roots. The VIII enters by two roots so close together that they may be treated as one, somewhat ventral and caudal to the lateral line VII. The VIII fibers enter the lateral acusticum nucleus and a part of them end, with or without branching, in connection with the spindle cells in various parts of the lateral nucleus as described above. All of the remainder apparently undergo bifurcation, the branches passing forward and backward. They are best traced in longitudinal sections. The caudally directed fibers run to the caudal end of the acusticum and some of them pass beyond the level at which the acusticum is differentiated and enter the nucleus funiculi. Such fibers as do this may be considered as homologous with the spinal VIII tract of *Acipenser* and of higher vertebrates. The fibers which pass forward run chiefly in or over the surface of the dorso-median nucleus and a very large part of them enter the cerebellum, where they end in the granular layer.

In sagittal sections through the lateral wall of the medulla the lateral line X root is seen passing upward and forward through the caudal bundles of VIII fibers (Fig. 30). The fibers of this root all enter the dorso-median nucleus and, I think, end in it without running forward or backward as far as the VIII fibers. No bifurcating fibers have been found either in this or in the lateral line VII root.

The lateral line VII (Figs. 1, 11, 11 a, 12, 29, 30) has two distinct roots of medium coarse and very coarse fibers, one cephalo-dorsal to the other. The ventral root runs close over the dorso-cephalic surface of VIII. Its fibers end in part among the ordinary cells of the lateral nucleus, but most of them pass into the dorso-median nucleus, while a few small bundles enter the lobus lineae lateralis (Fig. 11 a). A considerable number of these fibers pass forward through the outer part of the median nucleus and enter the cerebellum. I have not found any of these fibers turning backward.

The dorsal root is directed much more dorsally as it enters

the medulla and the greater part of it runs in the form of dense, closely defined bundles into the lobus lineae lateralis (Fig. 11 a). As the root passes through the dorso-median nucleus several small bundles branch off and end in that nucleus. A very considerable number of these fibers do not join the main bundles but enter the lateral nucleus, take the deep stain characteristic of the fibers which end upon the spindle cells, run as a loose bundle to the cephalic end of the acusticum and end upon the spindle cells there situated. The greater number of the spindle cells in this position are connected with the lateral line fibers, although some fibers seem to come to them from VIII.

The course of the spinal V tract (Figs. 1, 9-13, 29, 30) has been sufficiently described. A part of the fibers of the V root, however, do not run in the spinal V tract. Some very coarse fibers which come from the ramus ophthalmicus V run in the median part of the acusticum. They are not always well impregnated but in both sagittal and transverse sections they are traced to the caudal end of the acusticum and some of them may enter the nucleus funiculi. They are not shown in the figures. Other fibers of V bifurcate on entering the medulla (Fig. 29), one branch going to the cerebellum, the other running in the spinal V tract. Still other fibers run directly to the cerebellum without bifurcation. In one case a fiber which apparently belonged to V was seen ending upon a spindle cell as the VIII fibers do.

4. The cerebellum (Figs. 2, 12, 22).

The cerebellum consists of an inner cell layer and an outer fiber layer. The cell layer is a direct continuation cephalad and mesad of the two chief nuclei of the acusticum, the dorso-median nucleus taking the more important part. The fiber layer consists in part of a continuation of the cerebellar crest covering the outer surface of the acusticum, and in part of fibers of the VIII and lateral line VII nerves. These two layers are to be compared with the granular and molecular layers of other vertebrates but it must be noted that the PURKINJE cells do not lie between these two layers but are scattered through the inner layer. The fiber layer forms a thick dorsal commissure

which extends forward somewhat into the aqueduct. Beneath it there is a small and inconspicuous commissure formed of very fine fibers which collect in the median acusticum nuclei just as they come together in the cerebellum. The fibers of this small commissure enter the fiber layer after crossing. The two commissures are probably homologous with the commissure of fine fibers in the molecular layer of *Acipenser* which arise from the granule cells and enter the cerebellar crest of the other side.

The cells in the cerebellum are almost identical with those in the dorso-median nucleus of the acusticum. There are relatively large cells ($10-18 \times 20-32 \mu$) which form a layer adjoining the cavity and send their dendrites out into the fiber layer. As may be seen from Figs. 11 and 22, these cells closely resemble cells similarly placed in the acusticum. Other cells measuring $12-16 \times 16-24 \mu$ are found in the outer part of the cell layer (Fig. 12 left). The neurites of many of these cells are very readily traced in sagittal sections (Fig. 22). Both the cells adjoining the cavity and those lying in the outer part of the granular layer give off neurites of medium thickness from the base of one of the dendrites. The neurites run ventrally and slightly forward, form a loose bundle and enter the wall of the mid brain, where they descend to the ansulate commissure. I believe that they cross here and run to the tectum, as do some of the arcuate fibers in the brain of *Acipenser*. Other cells lying in the ventro-lateral part of the cerebellum near the junction with the acusticum, send their neurites more directly ventrad to cross to the opposite side with the arcuate fibers from the acusticum. Thus the internal arcuate fibers from the acusticum and cerebellum form a continuous series extending forward to the ansulate commissure, and there is so gradual a transition from the fibers of the acusticum to those of the cerebellum that the two can not be distinguished unless they are traced to their cells of origin.

In all parts of the granular layer there are found very small cells ($6-9 \times 8-12 \mu$) whose dendrites are longer and straighter than those of the small cells in the acusticum but do not extend beyond the limits of the granular layer (Fig. 12). Although

I have been unable to trace their neurites, I have no doubt that they are the granule cells and that the fine fibers of the molecular layer and cerebellar crest are derived from them.

The fibers which enter the cerebellum have been partly described. The VIII fibers are dichotomous branches of the root fibers and are relatively fine. They run along the outer surface of the acusticum nuclei or through the dorsal nucleus and through the inner part of the molecular layer of the cerebellum. They do not end in this layer but bend inward to break up in the granular layer. The lateral VII fibers are very coarse, run deeper in the cerebellum and enter the granular layer directly. No part of them is ever seen in the molecular layer. The relatively small number of V fibers entering the cerebellum are mingled with the VIII and lateral line fibers so that their course can not be separately traced. In addition to the above, a part of the tract from the lobus inferior, tractus lobo-cerebellaris, ends in the cerebellum.

From this description of the minute structure of the cutaneous centers the following conclusions may be drawn in addition to those noted above:

(1) The cell elements or neurones in the nucleus funiculi, acusticum (excepting the spindle cells), and cerebellum are apparently identical.

(a) Large cells with well developed dendrites and with neurites which become internal arcuate fibers. These are to be regarded as the primitive cells from which PURKINJE cells have developed in the cerebellum and acusticum of selachians and ganoids and in the cerebellum of other vertebrates.

(b) Small cells homologous with the granule cells of the cerebellum of higher vertebrates and similar to the granule cells found in the acusticum of *Acipenser*.

(c) Cells of the II type have not been found in any of these nuclei in *Petromyzon*.

(2) There is actual continuity of tissue between all these centers, and the fibers of the VIII nerve probably end in all of them. The fibers of the lateral line VII end in the acusticum and cerebellum, and those of the V end in the nucleus

funiculi, nucleus of the spinal V, cerebellum, and probably also in the acusticum.

A discussion of the general significance of these facts is reserved for the theoretical part of this paper.

d. Internal arcuate fibers.

The course of the internal arcuate fibers from the several cutaneous centers has been described in part. In the caudal part of the medulla the fibers coming from the nucleus funiculi, nucleus trigemini spinalis, and the acusticum course around the periphery of the medulla and cross the ventral raphé near the surface. These fibers are relatively fine and very numerous and form a conspicuous layer in the caudal part of the medulla, but grow relatively less numerous farther forward. In the cephalic part of the medulla the arcuate fibers are coarser and run deeper, crossing a little beneath the floor of the ventricle. Among these are the thick fibers from the spindle cells. The arcuate fibers can not be traced forward as a distinct tract, and in the tectum the tractus tecto-bulbaris and bulbo-tectalis are only imperfectly separated. I believe, however, that the relations of the arcuate fibers are the same here as in *Acipenser*.

e. The fasciculus communis center.

As in *Acipenser* the fasciculus communis system is represented in the medulla of *Petromyzon* by a vagus lobe extending from the caudal end of the medulla to the level of the IX nerve, and by a bundle of fibers extending forward from this to the root of VII, the sensory root of which constitutes the bundle. Caudally the vagus lobes are connected above the ventricle by the commissura infima HALLERI, and there continue into the cord median tracts of fibers which seem to be related to the vagus lobes alone.

In the cord in the region of the first and second spinal nerves a few cells situated in that part of the gray matter which represents the dorsal horns send dendrites into both the deeply staining and pale tracts. Other cells, situated nearer the median line, dorsal to the central canal, send dendrites into the pale tracts alone. Farther forward the latter cells become sharply distinguished in form and size ($8-32 \times 30-80 \mu$) from the cells

of the nucleus funiculi, which no longer send dendrites into this median dorsal region. The great majority of these cells, which constitute the vagus lobe, are situated close to the central cavity. Some of them are compact but with very rough or irregular bodies, while others are greatly elongated (e. g. $8 \times 80\mu$). Behind the commissura infima HALLERI some cells lie in or near the middle line and send their dendrites to both sides. These are to be regarded as belonging to the median nucleus of CAJAL. The dendrites are relatively short, thick, very profusely branched, and the final branches are very slender sinuous twigs. The great difference of form between the cells of the lobus vagi and those of the nucleus funiculi is shown in Fig. 21. The neurites are traced laterally and ventrally into the lateral tracts. The fibers are fine and in most parts of the lobe are not sufficiently numerous to form a bundle, so that it has been impossible to trace them to their destination. They do not bend in the direction of the arcuate fibers.

The sensory fibers of X are mingled with the motor fibers at their external origin, and after entering the medulla the sensory fibers can not be traced in haematoxylin sections. In GOLGI sections they are seen to run up from their point of entrance on the lateral surface of the medulla through the outer part of the nucleus funiculi to enter and end in the lobus vagi. The sensory IX runs deeper in the nucleus funiculi and acusticum.

The communis VII (Figs. 1, 11, 11 a, 29, 30) is extremely difficult to study owing to the fineness of its fibers, the compactness and complexity of the root and ganglionic complex, and the fact that the VII fibers are scattered in very small bundles which must pass through the spinal V tract and the acusticum to reach the front end of the vagus lobe. There is to be noted first what appears in a single haematoxylin series to be a strong general cutaneous component entering the spinal V with VII. The fibers are fine and I am in doubt whether they are general cutaneous and not rather communis fibers which pass through the spinal V in a very much dispersed condition. Some of the communis fibers of VII do thus pierce the dorsal part of

the spinal V tract, and others pass through the lateral nucleus of the acusticum and the space separating this nucleus from the spinal V tract. A considerable bundle of fine fibers collects above the inner border of the spinal V and a little further caudally this appears as a larger bundle above the internal arcuate fibers from the acusticum. This bundle runs caudally mesial to the acusticum until it joins the front end of the vagus lobe. The course of this root has not been described by previous authors. Its manner of entrance, through the spinal V nucleus, corresponds to that of the sensory IX and X roots.

The sensory VII, IX, and X roots are not large and the whole fasciculus communis system is poorly developed in comparison with the same system in *Acipenser*. It is a noticeable peculiarity that the vagus lobe is an important body of grey matter at the level of the commissura infima HALLERI and continues for some distance caudally from that. It is caudal to the commissure that the largest bundle of secondary tract fibers is to be found. The calamus scriptorius and the commissura infima HALLERI are very far forward with respect to the IX and X roots and the body of the vagus lobe. At the very caudal end of the medulla, at the point at which the canal shows the slightest enlargement, I have noticed in one series a bundle of fine fibers passing from the region of the fasciculus communis (cervical bundle) close over the lateral surface of the cavity and spreading out in the latero-ventral tracts. These are possibly collaterals of the fibers of the median dorsal tracts. It is possible that there is a mingling of the dorsal tracts proper with the cervical bundle in the cord and that these collaterals come from the cutaneous fibers. Such a mingling would explain also the fact that certain cells send their dendrites into both the dorsal tracts and the tracts which belong to the fasciculus communis system.

(f) The lower olive (Fig. 6).

This body presents about the same appearance in *Petromyzon* as in *Acipenser*, but is smaller. It consists of a group of spindle shaped cells disposed in the transverse plane parallel

with the ventral surface of the medulla and surrounding the roots of the XII nerve.

B. The Mid Brain.

a. Tectum opticum (Figs. 2, 12, 13, 14, 30).

As already noted, the caudal part of the tectum presents the characteristic appearance of the bi-lobed fish tectum, the two sides being connected by the dorsal decussation. In its cephalic part the two lobes become separated, there is no dorsal decussation, and the roof is a choroid plexus. The plexus grows wider cephalad as the lateral walls recede and the tectum disappears at the level of the posterior commissure.

The tectum presents a well defined grey zone adjoining the cavity made up of from three to six closely packed layers of cells, and a fiber zone which makes up more than three-fourths of the thickness of the wall. The fiber zone contains a large number of cells scattered irregularly through it. Upon the outer surface of the tectum throughout its whole extent there are isolated cells at short intervals which are pyramidal or balloon shaped, with the large end against the limitans externa and the smaller end penetrating the fiber zone. The tectum has a much larger number of cells in proportion to its whole volume or the volume of its fiber zone than there are in *Acipenser*.

The cells of the tectum are not so well differentiated as in *Acipenser*, but some of the same types are to be recognized. The cell and fiber zones are not distinguished in GOLGI preparations and for the study of the minute structure the cells may be divided into two groups, deep and superficial cells. The deep cells are vertical or horizontal. The vertical cells have ovoid or spindle shaped cell bodies which are usually within the cell zone and sometimes have central processes reaching the cavity. Their dendrites are few in number and rise toward the periphery. These resemble the cells denominated "type A" in *Acipenser* but are not so well differentiated. The neurites are not well impregnated and usually appear as only short stumps starting toward the surface, but in a single case a well marked short neurite was found well impregnated. The dendrites branch

more freely in the inner part of the tectum and do not have the extravagant end-bushes which are found on the type A cells in *Acipenser*. The two cells probably belong to the same category and the reason for the less marked differentiation in *Petromyzon* is to be found in the fact that the optic tract fibers are not confined to the outer zone as in *Acipenser*.

The horizontal cells are much more numerous than the vertical. They either have a single dendrite going off from the peripheral end of the cell and soon dividing into two large branches which are disposed horizontally, i. e., parallel with the internal surface of the tectum, or they are bipolar with the two dendrites disposed horizontally. Occasionally they are multipolar or stellate. They are larger than the vertical cells, the dendrites have a wide expansion, and these appear to be the most important elements in the tectum. The neurite always arises from some part of the laterally directed dendrite and enters the bundles going through the lateral wall of the mid brain. Sometimes the dendrite becomes gradually transformed into a neurite after a long course. The unipolar cells are situated near the cavity and there is a progressive modification to the bipolar and stellate forms from within outward.

In the outer part of the fiber zone there are a few stellate or pyramidal cells with short very richly branched dendrites which are probably to be classed with the pyramidal superficial cells described below.

Some of the superficial cells have mitral shaped bodies with two dendrites going off horizontally from the inner end of the cell body. The dendrites run parallel with the outer surface and send their branches somewhat inward. The neurites arise from the laterally directed dendrites, usually by the dendrite changing into a neurite. These cells are to be compared directly with the deep horizontal cells. Occasional horizontal cells in the outer part of the tectum have short neurites (Fig. 12).

The pyramidal cells (Fig. 13, 25) are somewhat more numerous than those last described and are more sharply characterized than any other cells in the tectum. The larger end

of the body stands at the outer surface of the tectum, and from the inner end arises a dendrite which immediately divides into a most complicated interwoven series of branches. The dendrites are short and their profuse division into small branches gives them a very characteristic appearance. It would be impossible to represent the more complicated of these cells in a drawing, that shown in Fig. 25 being extraordinarily simple. The neurite arises from some of the larger branches of the dendrite and breaks up in the near vicinity of the cell, but deeper than the dendrites. These cells probably can not be directly compared with any in the tectum of *Acipenser*.

The typical structure of the tectum as made out from GOLGI sections extends ventrally somewhat into the central grey of the lateral wall of the mid brain. This area may be compared with the *torus semicircularis HALLERI* of the brain of *Acipenser*, but its extent is not indicated in *Petromyzon* by anything in the gross anatomy as in *Acipenser*. The whole lateral wall of the mid brain forms a projection into the cavity, and this would be called the torus from the standpoint of gross anatomy. Only a small dorsal portion of it, however, belongs to the tectum and corresponds to the torus in *Acipenser*.

A large fiber tract (Figs. 13, 14, 15, 16), embracing the whole fiber zone, descends from the lateral border of the tectum through the wall of the mid brain. Before reaching the base of the brain the larger part of the tract turns backward and enters the medulla. The greater part of the remainder enters into the formation of the ansulate commissure and then joins the uncrossed tract to the medulla. A small cephalic portion of the tract from the tectum turns forward above the ansulate commissure and goes to the *lobi inferiores*. Whether there is any crossed tract to these lobes could not be made out.

The inner portion of the common tract just described consists of coarser fibers and these are especially evident in the ansulate commissure where a few of the large fibers from the spindle cells of the *acusticum* are impregnated among them. This inner coarse-fibered portion is doubtless made up of the internal arcuate fibers from the medulla as in *Acipenser*. The

outer fine-fibered portion runs along the ventro-lateral surface of the medulla and seems to extend into the cord. These are therefore the tractus bulbo-tectalis and tractus tecto-bulbaris respectively. Each has a portion crossing through the ansulate commissure, as in *Acipenser*. The tract passing forward is the tractus tecto-lobaris. The arrangement of all these tracts is simpler than in *Acipenser* and the tractus tecto-lobaris is much smaller and probably has no crossed portion.

From the cephalic portion of the tectum a few fibers enter the posterior commissure to cross to the opposite side. These are probably to be regarded as an isolated portion of the dorsal decussation, since they seem to enter the tectum of the other side.

The cells which accompany the optic tracts at the level of the posterior commissure and a little farther cephalad are far removed from the cavity and are all stellate and smaller than the horizontal or vertical cells of the tectum proper. I could trace the neurites of only two cells. One of these crossed to the opposite side in the posterior commissure, the other ran ventrad with the fibers of the commissure of the same side.

The nucleus which gives origin to REISSNER's fiber as described by SARGENT ('01) was not seen, although the fiber itself is very distinctly seen in longitudinal sections (Fig. 2).

b. The central grey and posterior commissure (Figs. 15, 30).

The nucleus of the III nerve and the situation of three large cells which give rise to MÜLLERIAN fibers have been described above. The cells of the central grey probably belong to two distinct categories. Some are doubtless to be compared with the commissural and tract cells of the cord and medulla, others send their neurites to the posterior commissure. There is a considerable collection of cells adjoining the cavity just lateral and ventral to the commissure, and both these and a large number of more distant cells in the central grey of the thalamus and mid brain send their neurites into the commissure. Some cells scattered in the fiber zone also belong to this category. The neurites of these cells are always fine at their ori-

gin, often exceedingly so. They often continue as extremely fine fibers nearly to or even through the commissure. Usually they thicken into medium or coarse fibers before they enter the commissure, but a considerable number of fine fibers are found in both limbs of the commissure as far as they can be traced. The fibers turn ventrally and caudally after crossing and spread widely through the lateral walls of the mid brain. The diffuse arrangement of the fibers makes it very hard to trace them, especially as they become mingled with the tracts descending from the tectum. I have traced the fibers to about the caudal border of the mid brain and suppose that they are destined to make connections with the motor nuclei of the medulla. The posterior commissure thus constitutes an important, if not the chief path for fibers from the central grey of the mid and 'tween brain to the motor apparatus of the medulla. It thus forms part of the path for carrying descending impulses from the striatum. The cells of the central grey which contribute fibers to the posterior commissure constitute the nucleus of that commissure, homologous with the nucleus described by KÖLLIKER in mammals (*Gewebelehre*, p. 445).

The end-nucleus of MEYNERT'S bundles, a part of which lies in the central grey, will be described in the following section.

c. *Commissura ansulata* (Figs. 13, 14, 30).

This commissure is not as complex as in *Acipenser*. I have demonstrated only the tractus tecto-bulbaris and bulbotectalis, including the neurites of the spindle cells in the acusticum and those of the PURKINJE cells in the cerebellum. It is altogether probable that the neurites of commissural cells and of the cells of the nucleus of MEYNERT'S bundles are present also.

C. ' *Tween Brain*.

a. Ganglia habenulae, epiphysis, and bundles of MEYNERT (Figs. 14-17, 30).

The general relations of these structures have been sufficiently described above. The greater size of the right ganglion habenulae is due to greater volume of both cells and fibers.

There is a central fiber mass in the right ganglion surrounded both internally and externally by a thick zone of cells. On the left side there is a slight internal collection of cells, but throughout most of the ganglion cells and fibers are mingled.

The cells in both ganglia closely resemble those in the same ganglia in *Acipenser* (Fig. 16). They are pyramidal, uni-polar cells which give off the neurite from some part of the dendrite. The neurites collect in the caudo-lateral angle of each ganglion to form the bundle of MEYNERT. The right bundle is very much larger than the left and contains both fine and medium fibers. In general the coarser fibers arise from the cells of the ganglion while the fine fibers end by short branches in all parts of the right ganglion. Some of the coarser fibers end in the ganglion, however, and a few fine ones arise there. The bundles take the usual course through the walls of the mid brain, the large right bundle lying closer to the cavity than the left, but not causing a ridge on the internal surface as in the species described by AHLBORN. Both bundles are very far removed from the cavity in the lower part of their course (Fig. 16). The bundles arrive at the ventral surface of the mid brain just behind the corpus mammillare and, making a turn mesad at nearly right angles, begin to decussate. At the same time a large bundle of fine fibers constituting nearly one third of the right bundle leaves the ectal surface of that bundle and continues caudally (Fig. 16). A few fine fibers continue caudally from the left bundle and become arranged in a definite fasciculus farther caudad. The details of the decussation are difficult to make out owing to the fact that in all my GOLGI preparations nearly all the fibers are impregnated. Sufficient can be made out, however, to show that the main features of the decussation and the place of ending are the same as in *Acipenser*. There is a large nucleus in the same position as the end-nucleus in *Acipenser*, extending caudally from the decussation of the III nerve at either side of the ventral groove of the ventricle to the level of VIII. At the level of III there is a considerable collection of cells between the decussation of III and that of MEYNERT'S bundles which probably belong to

the end-nucleus, and perhaps represents the corpus interpedunculare of authors. All the rest of the nucleus consists of cells closely adjoining the ventricle as in *Acipenser*. Caudal to the decussation the bundles of fine fibers at the right and left continue close to the ventral surface, at first diverging and then approaching one another. In both GOLGI and haematoxylin sections there appears a second decussation some distance behind the first, formed by the bundles of fine fibers (Fig. 2). Caudal to this second decussation, which reaches nearly to the end of the nucleus, there is still a very distinct small compact bundle of fine fibers on the right side. This continues caudally, crosses as a bundle to the left of the raphé, and runs on nearly to the caudal end of the medulla. The course of this bundle, together with the existence of the second decussation formed by the fine fibers, indicate that the fibers are being distributed to their endings and it is therefore difficult to believe that they are the fine fibers which end freely in the ganglion habenulae. They are traced much farther caudally here than has before been done. There is a certain similarity between this bundle and the *bundle x* described in *Acipenser* and the question arises whether that bundle may not after all be the continuation of the bundles of MEYNEK. I regret that a comparison of the *Acipenser* and *Petromyzon* preparations throws no further light on this question.

AHLBORN traced these bundles only to the point which I have spoken of as the second decussation, and did not recognize an end-nucleus. I have suggested ('01 c, p. 99) that the end nucleus may be regarded as a special group of slightly modified commissural cells. The greater elongation of the nucleus in *Petromyzon* and the fact that the bundles extend through nearly the whole length of the medulla lend support to this view. It seems probable that as the bundles pass backward in the medulla the fibers gradually find endings in relation with the commissural cells.

AHLBORN describes tracts entering the ganglia habenulae from the thalamus and from the lateral expansions of the fore brain ("hemispheres"). F. MAYER ('97) describes only the

latter (from the "Hirnrinde") as ending in the ganglia habenulae, and describes other fibers from the thalamus as passing through the superior commissure to end in the olfactory lobe. A discussion of these tracts is reserved until after the description of the fore brain, only stating here that the tractus olfacto-habenularis are the only tracts entering the ganglia habenulae besides the bundles of MEYNERT. The two tracts are about equal in size as they enter the ventro-cephalic angles of the ganglia, while the superior commissure does not appear to be much larger than one tract alone. The right bundle as it enters the ganglion divides into a number of bundles which make up the greater part of the central fiber mass and spread into all parts of the ganglion. The bundles have a general course toward the middle line but decrease greatly as they approach it. The larger part of the left tract goes directly to the commissure. This disposition of the tracts indicates that the greater part of both right and left tracts end in the right ganglion. This is clearer than in *Acipenser* and the asymmetry is greater, but in essentials the two forms agree.

Unfortunately there is no impregnation of fibers or cells in the epiphysis or Zirbelposter and I can give only a few observations on haematoxylin sections. The general relations of these structures have been described above. The extremely attenuated stalk of the epiphysis is too small to contain any considerable number of fibers. No fibers are to be seen in haematoxylin sections and, indeed, in some preparations the stalk seems to be completely obliterated in its caudal part. The tract which F. MAYER ('97) figures as running to the posterior commissure is impossible in *Lampetra*. The epiphysis itself is a vesicle whose cavity is largely obliterated by the thickening of its walls. The ventral wall is considerably thickened in two longitudinal ridges, one at either side of the hollow stalk. This wall is composed of a single layer of columnar cells which are higher in these two ridges. Among the bases of these cells are a few stellate cells having the appearance of nerve cells as STUDNICKA ('00) describes. The nuclei of the epiphysis cells have taken a distinct chromatic stain in iron haematoxylin. In

the ventral wall are seen a large number of bodies of about the same size as the nuclei which have a homogeneous grayish brown color. These resemble the nuclei of glia cells. The dorsal wall is likewise composed of a single layer of columnar cells, but these are so high as to meet the ventral wall in most places and so nearly obliterate the cavity. The cells are extremely long and slender, almost like fibers, and have their nuclei in slight enlargements either near the dorsal (basal) ends or near the middle. Between the dorsal and ventral walls, probably connected with the cells of the ventral wall, are a number of darkly staining bodies which appear to be the "rods or cones" described by STUDNICKA ('00). The structure of the epiphysis as a whole strikingly reminds one of the lens of the eye at an early stage of development.

Beneath the epiphysis lies the Zirbelpolster which is also an elongated vesicle. It is connected with the left ganglion habenulae by a band of fibers as previously described. This vesicle has a very thin dorsal wall consisting of about two layers of small cells, which passes gradually into a ventral wall consisting of many layers. This wall gives the appearance of a very dense mass of nerve cells such as is sometimes found in the brain of lower vertebrates. The vesicle has a large open cavity. From among the cells of the ventral wall nerve fibers emerge ventrally and form the band which runs to the left ganglion habenulae. The bundle is large and easily followed into the ganglion where it penetrates the cell layer and does not go to the superior commissure. This apparatus, therefore, is related wholly the left ganglion.

RETZIUS ('96) has studied the epiphysis and paraphysis of *Ammocoetes* by the GOLGI method and concludes that the epiphysis contains no nerve elements, while the paraphysis contains bipolar cells in its ventral wall which send fibers into the ganglion habenulae. He concludes: "In Anbetracht der interessanten regelmässigen Gestalt dieser bipolaren Zellenelemente und ihrer centralwärts ziehenden Fortsätze scheint mir die Paraphysis der *Ammocoetes* eher als die Epiphysis als ein functionierenden Hirnthiel aufzufassen zu sein."

STUDNICKA ('00) has described sense cells bearing rods or cones in the epiphysis. These are probably present in Lampetra, as noted above. He describes the paraphysis as only a pouch of the choroid plexus with a single layered wall throughout and containing no sense cells. This description will not apply in any particular to the Zirbelpolster of Lampetra, and I know of no other structure in this region of which STUDNICKA could be speaking.

In addition to the structure of the epiphysis and paraphysis, their position and the structure of the overlying tissues should be taken into account in order to determine their function. The epiphysis is separated from the paraphysis by a thin and imperfect membrane. The epiphysis is covered dorsally by the skeletogenous layer of the cranium, the outer portion of which is connected with the myocommata. This is a thick layer of fibrous connective tissue, containing many flattened and stellate nuclei. The layer is thicker here than elsewhere and in GOLGI sections there are seen many nerve fibers on their way to the skin. Immediately outside of this layer is a layer of pigment cells which form a dense and continuous pigment layer everywhere except in the cornea of the eyes and here over the epiphysis. Outside this is the thinner connective tissue layer of the dermis, and outside that the epidermis which is thicker and better supplied with free nerve endings here than elsewhere. The epidermis contains many deeply stained goblet cells which are lacking over the epiphysis. These facts show that provision has been made here for the passage of light as in the case of the lateral eyes, although the thickness of the layers offers greater resistance than in the cornea. The form and structure of the epiphysis make it an organ for focussing the light, although not as efficient as the lens of the eye. Finally, the nerve cells of the paraphysis are doubtless capable of receiving stimuli from the light which easily passes through the thin dorsal wall and cavity filled with fluid. These light stimuli would then be carried to the left ganglion habenulae. The fibers from the paraphysis seem to be more than half as numerous as those which end in the left ganglion from the tractus olfacto-haben-

ularis. It is possible to suppose that at one time the chief function of the left ganglion was in connection with this parietal eye. The whole apparatus can at present be nothing more than a light-percipient organ.

b. The thalamus.

The contribution of neurites from the central grey to the posterior commissure has been mentioned above. The remaining cells of the thalamus probably send their neurites caudally without crossing. Both categories of cells serve as part of an end-nucleus for fibers from the striatum. I have not found any special nuclei in the thalamus.

c. The hypothalamus (Figs. 17, 17 a, 18, 19).

The hypothalamus consists of inferior lobes, corpus mammillare, and saccus vasculosus. No one of these parts is as large in proportion to the rest of the brain as in *Acipenser*. The inferior lobes constitute the thick lateral walls, the corpus mammillare forms a thin walled caudal projection, while the saccus forms a thin floor for nearly the whole length of the hypothalamus. The cells of the hypothalamus are not as highly differentiated as in *Acipenser*, those of the inferior lobes as well as those of the mammillare presenting essentially the same characters as do those of the mammillare in *Acipenser*.

The inferior lobes have an inner cell zone and an outer fiber zone, which are not so well defined as in *Acipenser* owing to the peculiar form of many of the cells. The cells are all bipolar with a central process reaching the cavity between the ependyma cells and a peripheral process in the fiber zone. The cells present all gradations between two extreme forms. In one the cell body stands near the cavity and the central process is very short; in the other the cell body stands far from the cavity and the central process is very long. In the latter case the cell body may lie in the middle or dorsal part of the lobe and the central process reach the cavity at or near the ventral border of the lobe. The process may present all the characters of an ordinary dendrite, and may even be given off as a branch from a large dendrite. The dendrites are not richly branched but consist of a single long axis or of two or more long slender

branches with small offshoots. These main branches extend far laterad or dorsad in the walls of the inferior lobes and may even reach the thalamus. Their position is determined mainly by the disposition of the fiber tracts among which they lie. The neurites are directed latero-dorsad, and incline caudad in the caudal part of the lobe and cephalad in the cephalic part. In the cephalic part of the lobe the neurites cross behind the chiasma, forming the greater part of the postoptic decussation. These, together with those from the middle and caudal parts of the lobes, which do not cross, pass upward and backward through the lateral walls of the thalamus and mid-brain, forming the large tractus lobo-bulbaris et cerebellaris. A small part of the tract enters the cerebellum and the remainder passes back into the medulla. The tract corresponds in every way to the tract of the same name in *Acipenser*, except that a relatively smaller part goes to the cerebellum.

The cells of the mammillare are smaller than those of the inferior lobes and both the central processes and dendrites are more slender. These smaller and more slender elements are found also along the ventral border of the inferior lobes, as in *Acipenser*, and in the postoptic recess. There seems to be no essential difference in the relations of the cells of the mammillare and the inferior lobes. The neurites from the mammillare proper form distinct paired bundles which pass latero-dorsad over the walls of the corpus and bend caudad in the base of the mid brain as the tractus mammillo-bulbares (Fig. 30). The fibers of these tracts are more slender than those of the tractus lobo-bulbaris, corresponding to the smaller size of the cells of origin, but the presumption is that the two tracts have essentially the same relations in the medulla.

In the connections between the hypothalamus and fore brain there seems to be one important difference between *Petromyzon* and *Acipenser*, namely, that only a small part of the ascending fibers run by way of the anterior commissure, the most crossing in the postoptic decussation. I have been unable to demonstrate fibers to the anterior commissure and the very small size of the commissure is reason for thinking that they

are very few in number. On the other hand, a bundle of considerable size comes out from the postoptic decussation and runs dorsad, crossing the internal surface of the optic tracts, and enters the epistriatum where its end-branching forms a very rich network of fine fiber twigs (Figs. 17 a, 18, 30). This represents the chief part of the ascending fibers of the tractus strio-thalamicus of other fishes. Its running by way of the postoptic decussation is peculiar to *Petromyzon*. Whether this tract crosses in the postoptic decussation or anterior commissure, it has the same connections and functions and should be called the *tractus lobo-epistriaticus*. The descending fibers from the olfactory nuclei to the hypothalamus, usually assigned to the tractus strio-thalamicus, come from the lateral expansions of the fore brain and from the nucleus thalæniæ, and end in all parts of the inferior lobes and corpus mammillare (Figs. 18, 19, 20). They should be given the name *tractus olfacto-lobaris*.

The saccus is very much smaller than in *Acipenser* and its study has been correspondingly difficult. In GOLGI sections no nerve or sense cells have been impregnated, but a few cells which show a close resemblance to the ependyma cells are stained. Nerve fibers running into the saccus from the inferior lobes have been stained in a number of preparations (Figs. 17 a, 18). Their internal connections can not be found in GOLGI sections, but in hæmatoxylin preparations the fibers are easily followed forward along the lateral angle of the postoptic recess to the level of the postoptic decussation when they bend abruptly dorsad and pierce the decussation to reach the central grey surrounding the ventral part of the cavity of the thalamus. This is the same region from which one of the saccus bundles in *Acipenser* arises, but it was not traced so clearly there as in *Petromyzon*. The bundle in *Acipenser* which has this course ends freely in the saccus, and it is to be concluded that the bundle in both forms arises from the central grey of the thalamus just above the chiasma, runs as a paired bundle along the ventral wall of the inferior lobes and ends freely among the cells of the saccus epithelium, its probable function being to control the secretory action of this membrane. The second saccus bundle of *Ac-*

penser which arises from the ciliated cells of the saccus and ends in the thalamus nucleus close to the nucleus of the posterior longitudinal fasciculus, I have not found in *Petromyzon*. Neither have I found the ciliated cells, although my preparations are scarcely fit for the demonstration of these elements. I think it probable that this tract, if present at all, is very small.

The postoptic decussations are smaller than in any other form which has been studied. They consist entirely (?) of fibers from the cells of the hypothalamus. These go to one of three destinations, epistriatum, cerebellum, or medulla.

The similarity of the cells of the inferior lobes and corpus mammillare, the origin of the tracts to the medulla from all parts of the hypothalamus, the common distribution of the descending tractus olfacto-lobaris, and the simple character of the postoptic decussations all indicate that the inferior lobes and the corpus mammillare are essentially a unit in *Petromyzon*. Their functional differentiation as shown by their structure and connections is still slight in *Acipenser*. The beginning of differentiation is seen in *Petromyzon* in the ending of the tractus tecto-lobaris in the inferior lobes alone.

D. Fore Brain.

The identification of the several parts of the fore brain must rest solely on the study of the minute structure, on account of the crowding and displacement of the cephalic and lateral portions by the pressure of the great buccal cavity. The growth of this organ has carried the olfactory pit around upon the dorsal surface of the head and the olfactory lobes and areas have been correspondingly bent upward and telescoped back upon the base of the fore brain, the striatum.

a. Corpus striatum.

The two nuclei of which the corpus striatum is composed are much more distinct here than in any other fish. The striatum proper forms the base of the fore brain in front of the chiasma and above the preoptic recess, and is continuous laterally with the ventral wall of the lateral expansions,

the olfactory areas. The epistriatum forms the dorsal half of the wall of the fore brain, extending from the thalamus immediately in front of and below the ganglia habenulae forward above the lateral cavities to the olfactory commissure. It is in direct connection ventrally with the striatum behind the lateral cavities (Fig. 18) and laterally with the dorsal wall of the olfactory area and lobe above these cavities. Thus, the striatum and epistriatum are continuous only at the caudal end of the fore brain. The shoving backward of the olfactory lobes and areas which resulted in the formation of a Y-shaped cavity has resulted also in splitting the striatum and epistriatum apart in their cephalic portion.

The cells of the epistriatum are arranged in two to four rows adjoining the cavity. The larger end of the pyramidal cell body is next the cavity and a large dendrite which arises from the apex divides into two or more large branches which expand in the fiber layer. The dendrites bear numerous small spines which are knobbed at the end (Fig. 26) in the manner characteristic of the epistriatum, inferior lobes, and tectum of *Acipenser*. These peculiar spines are found nowhere in the brain of *Petromyzon* except on the epistriatum cells. These cells are so closely similar to the epistriatum cells of *Acipenser* that it would be impossible to mistake their identity. The neurites form a diffuse bundle which descends through the lateral wall and end in the striatum proper (Figs. 18, 30). These fibers are to be compared with the short neurites of the epistriatum cells in *Acipenser*. The epistriatum is traversed by a large tract of fibers from the olfactory area, the tractus olfacto-habenularis (Figs. 17, 17a, 18). The tract is divided into many bundles by the dendrites of the epistriatum cells, the largest bundle running along the dorsal border of the epistriatum. At its cephalic end, near the olfactory commissure, fibers enter the epistriatum from the cephalic wall of the olfactory lobe. These are neurites of cells in the olfactory lobe which stand in connection with olfactory fibers in the glomeruli, i. e., part of the olfactory tract. They come chiefly or wholly from the lobe of the opposite side through the olfactory commissure and end in

the epistriatum, constituting about half of the fibers which end there.

The cells of the caudal part of the striatum proper (Figs. 18, 19) are placed near the cavity and arranged in rows as are the cells of the epistriatum. The cell bodies are stellate or fusiform and some have central processes which run to the central cavity. The fibers from the epistriatum are the only ones which I have found ending in the striatum. The neurites pass backward from the striatum to end in the thalamus. I have not found these neurites going to any other region than the central grey of the thalamus (and mid brain?). They do not enter the hypothalamus. This renders it probable that the striatum fibers are distributed to the thalamus alone in *Acipenser*, where it was impossible to determine this point owing to the union of fibers from the striatum and olfactory area in one tract.

b. Area olfactoria.

This includes the whole caudal portion of the lateral expansions of the fore brain (Figs. 1, 18, 30). The wall is of about equal thickness throughout and consists of a central mass of cells and fibers with only a thin peripheral fiber zone free from cells. The cells are numerous, are stellate or bipolar and have long dendrites spreading widely through the whole wall. The whole area is penetrated by fibers from the olfactory lobe, many of which are traced with perfect ease in all my preparations. Most of the cells send their neurites upward and backward into the dorso-caudal part of the area where they collect into a large tract at the junction of the olfactory area with the epistriatum and thalamus. Here the tract bends around the sharp angle made by the junction of these parts and runs caudo-dorsad through the epistriatum into the ganglia habenulae, where it ends as described above (Figs. 16, 17, 18). This is the largest part of the tractus olfacto-habenularis.

The remainder of the neurites run from the ventral wall of the olfactory area through the striatum into the hypothalamus as the tractus olfacto-lobaris described above (Figs 18, 30).

c. Nucleus thaeinae.

The olfactory area is closely related over the outer surface

of the striatum with the nucleus thaeinae which makes up the wall of the preoptic recess (Fig. 20). The cells of this nucleus closely resemble those of the same nucleus in *Acipenser*. They are fusiform or stellate cells having central processes to the cavity and their dendrites spread widely. The nucleus on the whole appears so much like the mammillare, or that part of the inferior lobes which surrounds the postoptic recess, that in studying sections the optic chiasma appears to be only an interruption in a continuous nucleus. The neurites of these cells in part pass backward over the chiasma into the inferior lobes and in part pass dorsad to join the tractus olfacto-habenularis. These fibers are dispersed in the wall of the thalamus until they are about to meet that part of the tract coming from the olfactory area, when they appear as a distinct bundle forming the caudal border of the tract. I have not traced fibers to the nucleus thaeinae from the olfactory lobes, but suppose that such fibers exist.

d. Lobus olfactorius.

The olfactory lobe shows a very low order of differentiation. Cells and fibers are not gathered in distinct zones, although the cells are more numerous near the cavity. In haematoxylin sections the glomeruli are prominent and appear to be sharply marked off from one another. The study of Golgi sections shows that this apparent separateness of the glomeruli is due entirely to the arrangement of the olfactory fibers in bundles and is not dependent in any way upon the form or disposition of the cells of the lobe. In fact, many of the bodies which appear to be glomeruli are no more than cross sections of large bundles of olfactory fibers.

The olfactory fibers as they enter the lobe gradually break up in the course of these large bundles which are penetrated by the dendrites of cells. These bundles of branching fibers with the dendrites which pierce them form the glomeruli (Fig. 19). A single glomerulus is thus sometimes of great size, running through the outer part of the lobe. The dendrites which enter into the formation of these glomeruli come from numerous cells which lie in all parts of the lobe, either near the central cavity

or among the glomeruli themselves, but which for the most part show no basis for grouping in classes. The most striking fact is that there are no well developed mitral cells to be found. There are, indeed, a few cells situated in the glomerular layer which are somewhat larger than the majority of the cells of the lobe, measuring $12-15 \times 17-22 \mu$. I have found only a very few such cells in all my preparations and never more than two in any one section although there are scores of other cells fully impregnated in the same sections. I have inserted into Figs. 19 and 20 drawings of four of the most characteristic cells of this type, and from the drawings it will be seen that they differ from the other cells of the lobe chiefly in the fact that their dendrites are directed outward to a restricted region of the glomerular layer, where they break up into a relatively large and dense end-bush. The branches of this end-bush are interwoven with the fibers of one of the large olfactory bundles. These are the characteristics of mitral cells in other vertebrates and the cells in question are to be considered as mitral cells, although they are very slightly differentiated from the other cells of the lobe.

The majority of the cells in the lobe are stellate or fusiform, measuring $10-12 \times 12-16 \mu$, are situated in all parts of the lobe except the glomerular layer, and have two or more dendrites which diverge and break up in widely separated parts of the glomerular layer. Large numbers of these cells are impregnated in all my preparations, and in almost every minute portion of the glomerular layer their dendritic branches are intricately interlaced, very numerous small branches entering and ending in the glomeruli. These cells are therefore the chief elements for receiving the olfactory stimuli. The neurites of the larger number of these cells pass backward through the lobe into the olfactory area, where they end in relation with the cells above described. The greater part of the course of many of these fibers can be traced in single sections in favorable planes. In the cephalic wall of the lobes many fibers turn towards the middle line and cross to the opposite side in the olfactory commissure. This commissure lies just beneath the extreme cephalic end of

the epistriatum and probably the larger part of the fibers entering the epistriatum from the olfactory lobe come from the opposite side in this commissure.

IV. THEORETICAL CONSIDERATIONS.

A. The Sensory Systems.

Since a complete study of the cranial nerves has not been attempted, there was included in the descriptive part only the course of the nerve roots proximal to their ganglia. The identification of the sensory centers, however, has been based upon the peripheral distribution of the nerves. The study of these nerves has brought to light some important facts, and sufficient description is given here to verify the account given of the roots and to serve as a basis for theoretical conclusions. The study was made upon haematoxylin and GOLGI series. The distribution of the chief rami was determined by the distribution of some branch or branches in each case.

a. The sense organs (Figs. 27, 28, 28 a).

There are two sets of sense organs on the head and branchial region of *Lampetra*. (The trunk region was not studied.) One of these is innervated by lateral line nerves, the other probably by fasciculus communis components. The lateral line organs are of the type called pit organs. The arrangement of these is shown in Fig. 28, which represents the lateral and ventral surfaces of the head, and the structure of one organ in Fig. 28 a. There is an irregular and incomplete paired ventral row extending through the branchial region and becoming regular and complete near the buccal cavity. In one specimen these rows were made up of forty-one organs on one side and fifty-four on the other. Continuing from the front end of this, a row of about thirteen organs runs laterally and forward parallel with the border of the mouth. At the caudal end the ventral rows bend laterally toward the last gill slit. Below and in front of the first gill slit is a group (not a row) of from three to six organs. Beginning at the ventral boundary of the cornea, within the border of the eye, and running upward and forward

is a row of nine or ten organs. A little nearer the mid dorsal line and separated from the cephalic organ of the last row by a double interval, a row of six organs continues forward to the tip of the snout. Caudally from the dorso-caudal border of the eye a row of nine organs extends backward and slightly upward to near the level of the first gill slit. Several (four) more organs extend caudally at the same level but at longer intervals. Just above and between each two gill slits occur one or two organs. Finally, near the mid dorsal line an irregular paired dorsal row of nine or ten organs extends through the gill region up to the level of the pineal gland.

In surface view, under a dissecting lens these organs present a very characteristic appearance. The whole organ is somewhat oval in outline, the long axis being in the direction of the row of organs, and is bounded by a distinct whitish or opaque lip or ridge. This ridge is broad and thick at the two sides and is very small at the two ends of the oval. From this it results that the ridges overhang and cover the greater part of the pit which appears in surface view as an elongated furrow or slit, usually narrower in the middle. In sections it is seen that the organ is raised up on a pronounced papilla caused by a thickening of the subcutaneous tissue which invades the space between the pigment and fibrous layers of the dermis. The ridge or wall of the pit is composed of the outer layer of the epidermis, which is very much denser here than elsewhere and is free from gland cells. This ridge is continuous with the supporting cells of the floor of the pit, and the sense cells form a barrel-shaped or elongated organ in the floor. It sometimes happens that two organs in a line are so closely set as to appear continuous in cross section and in other cases the single organ is much longer than broad, but in any single section the organs have a distinct barrel shape. The central part of the floor of the pit is slightly or considerably raised, so that the pit often appears rather as a deep and narrow ditch. The sense cells (which are stained an intense black in iron haematoxylin while the supporting cells are a grey blue) are spindle-shaped with pointed-ends converging at the surface. The peripheral end of

each cell bears a slight conical enlargement whose base forms part of the surface of the organ. There seems to be no hair or other projection. The nerve fibers supplying the organ come up through the thickened subcutaneous tissue and lose their medullation as they pass through the dermis. Up to this point they have the caliber of lateral line fibers and in GOLGI sections they appear thicker than the general cutaneous fibers. Surface precipitates have prevented the full study of these organs by the GOLGI method, but the branching of the nerve fibers about the bases of the sense cells was seen.

The second set of sense organs are the end-buds (Fig. 27). These organs do not produce a thickening or other externally noticeable mark in the epidermis, and in sections are to be made out only by the arrangement of their cells and the slightly deeper stain which these cells take. The end-buds are shaped like a goblet or wine glass from which the base is broken off. The body of the organ stands in the outer layer of the epidermis and the stem penetrates the inner layer. The stem consists largely of the nerve fibers which supply the organ. The organ consists of sensory and supporting cells. The supporting cells are cubical or rounded, have not the vacuolated appearance of the cells in the outer layer of the epidermis, take a deeper stain and are closely packed into a dense mass. Among the supporting cells are slender spindle-shaped cells with elongated nuclei which take a black stain. The cells are exceedingly slender and have the appearance of thick sinuous fibers. The outer end reaches the cuticula and the inner end, in some cases at least, reaches the inner border of the epidermis. In iron haematoxylin sections fine nerve fibers which stain an intense and characteristic blue are seen passing through the dermis and up along side of the sense cells. Similar fibers are seen in GOLGI sections although the sense cells are not impregnated.

The number and distribution of these organs over the whole head could be worked out from sections. A brief examination of sections indicates that there is probably no regularity in their distribution, although in the gill region there are more near the mid-dorsal and ventral lines than elsewhere. The total

number of these organs in about two millimeters in length of the body at the level of the first gill slit is about sixty. The organs are usually found singly, but often two, three or four are placed near together. In the anterior part of the head they do not appear to be more numerous than in the gill region.

b. The cranial nerves.

1. The vagus group (Figs. 7, 29).

After emerging from the wall of the medulla the mixed communis and motor roots of X run as four or five bundles for some distance within the cranial cavity, from which they emerge just within the caudal end of the auditory capsule. In transverse section the bundles in the cranial cavity appear in a dorso-ventral row, the most ventral being the cephalic root. As they near the foramen of exit these roots come close together and beyond the foramen they form a single nerve trunk which passes backward as the vagus proper. The IX nerve has a single communis root which runs parallel with the X roots in the cranial cavity, but outside of and below them. Immediately above it is the post-auditory lateral line root which is much larger than any of the IX or X bundles, and is laterally compressed and covers the outer surface of the X roots. As all these roots approach their foramina the IX becomes closely applied to the lateral line root and emerges through a separate foramen slightly dorsal to that for X. The lateral line root has still another more dorsal foramen, but the IX joins it again beyond the foramen. The lateral line root has a large V-shaped ganglion of large cells, one limb of which extends dorsally on the outer surface of the cranium while the other extends latero-ventrally. The root of IX accompanies this lateral limb of the ganglion as a well defined bundle of fibers which are connected with small cells forming the ventral part of the ganglion. The whole lateral limb of the ganglion is figured by AHLBORN ('84) as the ganglion of IX (*Br.* 1.). As it leaves its ganglion the trunk of IX receives a considerable bundle of fibers from the large cells of the dorsal part of the ganglion. These lateral line fibers are slightly thicker than the IX fibers, but can not be traced to their destinations in my preparations. It is probable that they innervate

pit organs of the ventral row as described by ALCOCK ('98). The vagus trunk also receives a large component of lateral line fibers from the VII-X anastomosis, as will be described below.

The post-auditory lateral line root sends the greater part of its fibers into the dorsal limb of its V-shaped ganglion. The lateral limb gives rise to one large ramus besides the fibers which enter the IX trunk. This ramus divides into two main branches and several twigs. One of the main branches runs outward, upward, and forward around the auditory capsule and innervates the lateral line organs of the post orbital row which passes ectal to the ear. The small twigs run laterally above the gill sacs and probably innervate some of the more dorsally situated organs on the side of the head. The dorsal limb of the lateral line ganglion receives the greater part of the VII-X anastomosis. The fibers of this anastomosis together with those from the ganglion form a longitudinal trunk which runs both forward and backward from this point. It is the *Nervus lateralis* (see discussion below). The caudal portion of this nerve, which lies lateral to the spinal canal throughout the length of the body, is well known. I have not seen any description of the cephalic portion. It extends forward from the upper limb of the ganglion above the auditory capsule, and presumably innervates the pit organs near the mid-dorsal line as far forward as the pineal gland. The lateral line nerve is thus composed of lateral line fibers with the possible exception of an almost insignificant number of *communis* fibers which it may receive from the VII through the anastomosis. The *communis* fibers which appear to enter the anastomosis from VII may be distributed to end-buds before that anastomosis joins the lateral line nerve.

That portion of the VII-X anastomosis which does not enter the *N. lateralis* passes down outside of the dorsal limb of the lateral line ganglion and joins the outer surface of the vagus trunk. It is presumably these fibers which innervate the pit organs of the ventral row, as described by ALCOCK. It is a very striking fact that these ventral organs in the gill region should be supplied by lateral line VII fibers, i. e., by pre- and

not post-auditory components. The interesting question arises, why a part of these organs should be innervated by post-auditory components running in the IX trunk.

The roots, ganglia, and rami of the vagus group are diagrammatically projected on Fig. 7, and shown in their proper relationship in Fig. 29.

2. The VII-VIII complex (Figs. 11, 11 a, 12, 29).

The roots of VII and VIII both enter the auditory capsule. The VIII has medium sized fibers and a large ganglion of very small cells, together with a few very thick fibers and large cells. The ganglion is dorso-ventrally flattened and is elongated. It is a dense mass of cells and fibers from which two main rami go to the cephalic and caudal portions of the ear. The two lateral line VII roots, arising higher on the wall of the medulla, come down close over the cephalic surface of the VIII roots and ganglion and, coursing forward and downward, make their exit from the capsule at the cephalic and mesial angle. The fibers are thick and are easily distinguished from those of VIII or the communis VII. The root bears a large ganglion of medium large cells, the greater part of which lie beneath the auditory capsule, extending both forward and backward. A part of the ganglion cells accompany the root in the foramen and within the auditory capsule. From this ganglion the VII-X anastomosis passes laterally and from the cephalo-lateral angle the large buccal trunk goes ventro-laterally to supply the pit organs of the infra-orbital line. The anastomosis contains a few fine fibers which pass through the ganglion, coming presumably from the ganglion of the communis root to be described below. As the anastomosis passes around the auditory capsule it gives off some fine branches which presumably innervate the pit organs above and in front of the first gill slit. Miss ALCOCK has described two other nerves from the front end of the ganglion which COLE ('98) interprets as otic and ophthalmicus superficialis. From the posterior portion of the ganglion arises the ramus hyoideus which divides into a branchial nerve to the hyoid segment and a ramus branchialis profundus as described by ALCOCK.

As the lateral line VII root is traced through the foramen in the auditory capsule, a compact bundle of finer fibers is seen in its mesial portion. These fine fibers are followed in among a group of very large ganglion cells which is crowded into the mesial angle of the auditory capsule, beneath the lateral line and VIII roots. The origin of the fine fibers from these large cells is entirely clear in both haematoxylin and GOLGI preparations. The cells are in part crowded among the fibers of the VIII root and numerous very fine fibers enter the medulla among the VIII fibers and pierce the acusticum and spinal V tract to reach the fasciculus communis as already described (p. 24). This is the root and ganglion of the communis VII which has been overlooked by all previous workers. The further course of this component peripherally I have been unable to work out in haematoxylin preparations owing to its small size.

3. The trigeminus.

This requires only passing mention because of its simple arrangement. The large sensory root emerges from the cranium through a foramen in front of the auditory capsule and bears a large ganglion of medium large cells, which is divided into nearly separate dorsal and ventral limbs. The dorsal limb belongs to the ophthalmic ramus, the ventral to the maxillary and mandibular.

The description of the sense organs and nerves shows that:

1. There are both lateral line organs and end-buds in the skin of *Petromyzon*.

2. The lateral line organs are numerous well formed pit organs, and have an arrangement very similar to that in other fishes. They are innervated by a special system of nerves which constitute rami or components corresponding for the most part to the lateral line nerves of other fishes. This system of nerves and its brain center are very large in accordance with the large number of end organs.

3. There is a large post-auditory lateral line root as in other fishes. This root supplies the larger part of the fibers for the innervation of the pit organs dorsal to the gill slits and on the trunk.

4. The N. lateralis is made up probably wholly of lateral line fibers derived from the post-auditory root and from the VII-X anastomosis.

5. The end-buds are comparatively few and the fasciculus communis system is consequently small both centrally and peripherally.

6. The communis VII root has essentially the same relations as in other fishes. It consists of fine fibres with very large ganglion cells which are characteristic of this root in fishes.

As the peripheral organs and nerves do not belong to the main subject of this study I shall not burden this part of the paper with an extended discussion of the literature of the cranial nerves of Cyclostomes. LANGERHANS ('73), as reported by AHLBORN, has described both lateral line organs and end-buds. AHLBORN ('83, '84) has given the fullest description of the nerve roots but has overlooked two important roots, the lateral line X (post-auditory) and the communis VII. There is apparently considerable difference in the number and arrangement of the roots of the vagus group between *Petromyzon planeri* and *Lampetra*. The roots are fewer in number in *Lampetra* and the IX is single and not the most cephalic. It is preceded by the post-auditory lateral line root, while in *P. planeri*, according to AHLBORN, the root which gives rise to the lateralis nerve follows the four rootlets of the glossopharyngeus. It seems certain, considering the position of the lateral line root in all fishes, that AHLBORN has made an error in analyzing the ganglia and roots, and that he did not properly identify the root or roots which give rise to the "R. lateralis vagi." The fact that he assigns the whole of the lateral limb of the lateral line ganglion to IX shows that the analysis of the ganglia and roots is not accurate. Since it is not possible that he should have overlooked so large a root as the post-auditory lateral line root, it is probable that it is represented by the first two of his IX roots, which arise higher up on the wall of the medulla than the others and enter the acusticus nucleus. AHLBORN does correctly state that the VII-X anastomosis joins the ramus lateralis and gives part of its fibers to the vagus proper.

In describing the VII root AHLBORN has entirely overlooked the fasciculus communis root and described only the dorsal root, which arises from a nucleus "welcher über den Acusticuskernen im obersten Rand der Hirnwand liegt, da, wo dieser im Begriff ist, in das Cerebellum überzugehen." This is, as shown above, a lateral line root and there is besides a more ventral lateral line root apparently overlooked by AHLBORN. The formation of the VII-X anastomosis from the ganglion of these roots has been properly described by AHLBORN. His failure to find the fasciculus communis root has misled later authors, especially with regard to the homology of the ramus lateralis vagi.

Miss ALCOCK ('98) has described the distribution of fibers innervating lateral line organs by way of rami of VII, IX and X, and reaches the conclusion that the lateral line nerves do not form a separate system but form an essential part of each branchial nerve. This contention ignores the whole tendency of recent investigations to analyze the cranial nerves into components according to their function, as shown by central connections and peripheral distribution, and requires no further discussion. Her description of the nerves I have verified for the most part, but there are certain additions and corrections to be made to her description of the roots from which the nerves are derived. She has overlooked the fact that the fibers in the vagus which supply lateral line organs are derived from the VII-X anastomosis, and hence have no relation whatever, morphological or physiological, with the fasciculus communis fibers, except that they happen to run in the same trunk. She does not describe the ganglion of IX or its relation to that of the lateral line nerve, although she clearly states that the latter is entirely distinct from that of X proper. If we assume that the conditions are the same as in *Petromyzon planeri* and *Lam-petra*, she has probably failed to analyze the ganglia of the post-auditory lateral line and IX roots and so failed to recognize the origin of the lateral line component of the IX trunk from a true lateral line root. It is certain that IX has no more connection with the lateral line system than X has. In describing

VII, Miss ALCOCK mentions only one root, and has overlooked the communis root. Failure to recognize this as a separate root gives an erroneous conception of the nature of the VII-X anastomosis and hence of the nature of the lateral line nerve.

COLE ('98) in criticizing this paper questions whether all the organs described by Miss ALCOCK are lateral line organs. The facts set forth in the present paper settle this question in Miss ALCOCK's favor so far as the identification of lateral line organs is concerned. It must be said that COLE was much more severe in his criticism than the known facts at the time warranted and that he took the wrong course in doubting the existence of lateral line organs and components where Miss ALCOCK had seen them.

COLE ('98 a) also questions the interpretation of the ramus lateralis vagi as a lateral line nerve, and this point requires somewhat fuller attention. STRONG ('95, p. 199), after quoting AHLBORN's description of the nerve roots in *Petromyzon*, says: "The first fact that impresses one in this arrangement is that the first set of roots from the Acusticus region do not form the N. lateralis, but the R. branchialis. Furthermore, the N. lateralis is formed partly by a recurrent branch of the Facialis passing around outside the auditory capsule—a thing which does not occur in the N. lateralis in higher forms. Again on comparing the course of the N. lateralis with the arrangement of the pits, it is evident that only a small proportion of them would be innervated by this nerve, which has a position near the mid-dorsal line. When these facts are considered—especially the non-derivation of this nerve from the Acusticus center, thus differing from the origin so universal for all other forms—it must be regarded as very probable that this nerve does not represent the N. lateralis vagi of higher forms. . . . What it does represent is probably the R. lateralis trigemini, so-called, of Teleosts—a nerve which is formed principally, as we have seen, by a recurrent branch of the Facialis, derived from the lobus trigemini [i. e., of Teleosts,—the cephalic part of the lobus vagi or fasciculus communis], and which is reenforced by a branch from the yagus. It would then much more probably innervate

the papillae which are so numerous on the dorsal fin, and which probably correspond to the structures innervated by the R. *lateralis trigemini*. The R. *branchialis* would probably represent the R. *lateralis*. I am forced to believe that the exact anatomy of these nerves is not yet accurately known, nor have their connections with the cutaneous sense organs been sufficiently worked out." It is evident that STRONG has been misled here by the imperfect description of the roots by AHLBORN. Not one of the considerations stated holds good when it is known that this nerve, including the recurrent branch from VII, does arise from the acusticum, that the pits on the sides and ventral surface of the gill region are innervated by other rami containing lateral line components, and that this nerve is probably destined for lateral line organs caudal to the gill region.

Following STRONG, but independently, COLE ('98, p. 179) comes to the same conclusion from the work of STANNIUS, AHLBORN, and RANSOM and THOMPSON ('86). COLE says: "It seems to me therefore that there is room for little doubt as to the morphological value of the '*lateralis*' nerve of *Petromyzon*, since all the known facts of its anatomy point to the conclusion that it belongs to the accessory lateral series. First, we know that its roots correspond to those of the accessory lateral system in higher Teleosts, and that besides its posterior or vagal rootlets, it has also an anterior or (trigemino-?) facial root; second, its fibers are of the same nature, being somatic sensory in function; and third, it is connected with the spinal nerves in a manner characteristic of the accessory lateral series, and such as to justify RANSOM and THOMPSON's description of it as a commissural nerve." The only point of any significance here, besides those adduced by STRONG, is the connection with spinal nerves described by RANSOM and THOMPSON. These authors, according to COLE, also state that the *lateralis* nerve has no ganglion. It must be said that if they were unable to find the ganglion, which constitutes more than two-thirds of the whole ganglionic complex of the vagus group, their evidence with regard to connections may be considered as of doubtful value until confirmed.

C. J. HERRICK ('00, p. 309) views the suggestion of

STRONG and COLE cautiously and suggests the possibility of this nerve containing both communis and lateral line fibers and showing gradual modifications such that it contains only the one or the other in certain cases.

The interpretations given by these authors rested upon insufficient knowledge of the structures concerned. The origin of the nerve as a post-auditory root (plus fibers from the VII anastomosis) from the acusticum and its distribution to lateral line organs put its homology with the ramus lateralis vagi of higher forms beyond all question. The position of the nerve offers no difficulty, since it arises (KUPFFER '95) as an epidermal thickening as in other fishes and sinks into its definitive position later. Its fibers probably reach their sense organs by way of the spinal nerves. These constitute the connections seen by RANSOM and THOMPSON and wrongly interpreted. The nerve has probably no relation whatever with the accessory lateral system. The position which it has secondarily assumed remains to be explained. It appears that the lateral line in *Petromyzon* has degenerated from a typical ichthyopsid condition, and the position of the nerve is connected with this degeneration.

As this paper is passing through the press I have had for the first time an opportunity to examine MERKEL's work "Ueber die Endigungen der sensiblen Nerven in der Haut der Wirbelthiere." His description of the histology and distribution of both lateral line organs and end-buds in *Petromyzon fluviatilis* agrees in all important points with that given in the present paper.

c. The sensory centers.

In regard to the centers of these sensory systems in the medulla, the chief interest lies in the light which the brain of *Petromyzon* throws on the relation of the cutaneous and visceral centers to one another and to the grey columns of the cord. In a paper on the brain of *Acipenser* ('01 c) the writer has argued that the general and special cutaneous centers are essentially a unit, although already highly developed and differentiated, and that they represent the dorsal horns of the cord, while the communis center represents structures in the cord mesial to the dor-

sal horns. The more primitive *Petromyzon* brain gives strong additional support to this interpretation.

It is interesting to note, first that the cutaneous centers are nearly as large, although not so well differentiated, in *Petromyzon* as in *Acipenser*. STRONG was led into error regarding the relative development of the cutaneous and visceral centers in *Petromyzon* by AHLBORN's imperfect description of the VII nerve. Following the quotation given above, STRONG says: "If the character of the so-called N. lateralis be as above supposed, the most dorsal nucleus of the Acustico-facialis center, from which the Facialis emerges, would correspond to the lobus trigemini." Here STRONG uses the term lobus trigemini in the sense in which it was applied in Teleosts, i. e. the cephalic part of the communis center. In that sense there is no lobus trigemini in *Petromyzon*, but only a very slender pre-auditory fasciculus which is distinguished with difficulty. In the sense in which the term is used in Ganoids and Selachians, however, there is a very well developed lobus trigemini (i. e. lobus lineae lateralis) which is the most dorsal acusticum nucleus and receives the dorsal lateral line VII root. This fact alone is sufficient to indicate the great development of the cutaneous centers.

The argument for the unity of the cutaneous centers was supported by the following evidence from *Acipenser* (OIC, p. 117):

(1) Continuity of tissue between the acusticum and cerebellum, the acusticum and cerebellar crest being exact equivalents respectively of the granular and molecular layers of the cerebellum.

(2) The fact that the root fibers of each of the cutaneous nerves, V, lateral line, and VIII, end in all three centers, nucleus funiculi, acusticum, and cerebellum.

(3) Identity of the nerve elements in all three centers,—large or PURKINJE, granule, and II type cells.

(4) The origin and development of the PURKINJE cells from the large cells of the acusticum and dorsal horns. This differentiation is in actual progress in *Acipenser* and the PURKINJE

cells are connected with the ordinary large cells by so many transitional forms as to remove all doubt of their origin.

(5) The fact that the secondary connections are the same for the dorsal horns and acusticum.

Similar evidence is found in the brain of *Petromyzon* :

(1) Continuity of the dorsal horns, acusticum, and cerebellum, there being even in this more primitive form, a slightly developed molecular layer and cerebellar crest which bear essentially the same relations to the granular layer, acusticum and lobus lineae lateralis as in *Acipenser*. The continuity of the dorsal horns with the special centers strengthens the argument very greatly, as it is what should be expected in a lower brain. The association is so close here that the nucleus funiculi is not well developed and the acusticum does not become a separate nucleus until a point in front of the IX root.

(2) The ending of general cutaneous fibers in the nucleus funiculi, nucleus trigemini spinalis, acusticum (?), and cerebellum; of lateral line fibers in the acusticum and cerebellum; and of VIII fibers in all three centers.

(3) The identity of the nerve elements in all the centers upon a lower plane than in *Acipenser*. In *Petromyzon* there are large cells and granules, while no II type cells have been found.

(4) The PURKINJE cells have not yet been differentiated. The cells in the cerebellum which correspond to the PURKINJE cells of higher forms are exactly like certain large cells which form the most conspicuous elements in the acusticum. These large cells in the cerebellum and acusticum have the same relation to the molecular layer and cerebellar crest respectively. Further, the primitive PURKINJE cells in the cerebellum send their neurites as internal arcuate fibers to the tectum as do the large cells in the acusticum. This leads to the next point.

(5) While in *Acipenser* only the dorsal horns and acusticum were shown to have the same secondary connections, this is clearly true in *Petromyzon* for the cerebellum also.

(6) The cerebellum in *Petromyzon* has reached a stage of differentiation only very slightly above that of the acusticum.

Except for one fact the cerebellum must be regarded as only a dorsal fusion or bridge between the two acustica. That fact is that a small bundle of fibers from the inferior lobes enters the cerebellum. This small bundle marks the beginning of differentiation of the cerebellum into a coordinating center, but its effect has not become appreciable in the structure of the cerebellum in *Petromyzon*. The very primitive condition of the cerebellum is well shown by the fact that no other tracts enter it from in front.

Emphasis has been laid on the continuity of the dorsal horn and acusticum, and the close similarity of the cells in the two is important. In this respect *Petromyzon* adds strong evidence at the point of the argument which necessarily has the least support in *Acipenser* or any higher brain. The separation of the medullary centers from the cord becomes greater in higher forms, and here in *Petromyzon* we have an approach to primitive conditions. The presence of a cerebellar crest and a lobus lineae lateralis throws a new light on the early condition of the cutaneous centers. It shows that the conditions in *Acipenser* and the selachians (?) are much more primitive than in the teleosts, not simply divergent. In the teleosts the cutaneous centers have become relatively reduced, the lobus lineae lateralis being absent, although the cerebellum has reached a higher development as a coordinating center. The presence of a molecular layer and cerebellar crest while the cerebellum is still a cutaneous center and not to any degree a coordinating center, suggests that the separation into granular and molecular layers is the earliest differentiation which appears in the somatic sensory centers. The molecular layer is made up chiefly of the neurites of granule cells which are characteristic connective elements in the cutaneous centers of all vertebrates. The *great* development of the molecular layer is connected with the exercise of the function of coordination. Only the front end of the cutaneous centers (cerebellum) takes on this function secondarily and in this region the PURKINJE cells develop. In lower fishes (selachians, ganoids) the effect is felt in the adjoining part of the acusticum and PURKINJE cells are developed there also. In

the dorsal horns PURKINJE cells are never developed for lack of a great number of granule cells and a large molecular layer.

The lobus lineae lateralis has little significance further than to give additional proof that this nucleus in selachians and ganoids is part of the acusticum. In *Petromyzon* it is more closely connected with the acusticum, while the cerebellar crest lies on the ectal surface of the lobe. This may be regarded as the primitive relation; in selachians and ganoids the crest came to lie between the lobe and acusticum by means of an infolding of the wall along the line of the crest. In higher forms both crest and lobe have disappeared.

The argument for the unity of the cutaneous centers of the cord and medulla could scarcely receive stronger support than has been derived from the comparative study of the brains of *Acipenser* and *Petromyzon*. The result has been to show that the centers for general and special cutaneous sensation present apparently much less differentiation and separation in fishes than exists between the peripheral organs themselves. The evidence is, I think, conclusive that these centers have been developed from a primitive dorsal horn of the cord-medulla in response to the development of the special cutaneous sense organs of the head.

JOHANNES MÜLLER (quoted by SCHAPER '99) thought that he saw in the lateral walls of the medulla (acusticum?) of *Petromyzon* the equivalent of the lateral part of the cerebellum of other fishes.

SCHAPER ('99 a) shows that the cerebellum of *Petromyzon* consists of granular and molecular layers and contains large cells which he thinks are true PURKINJE cells, although he has not demonstrated the characteristic spiny dendrites. He concludes that the cerebellum is to be considered "als völlig *gleichwertiges* Organ in die Reihe der Kleinhirne der übrigen Vertebraten." He further says: "Für die phylogenetische Betrachtung endlich ergibt sich hieraus, dass, wie EDINGER schon bei früherer Gelegenheit vermuthet hat, das Kleinhirn in der That einer der ältesten Hirnabschnitte zu sein scheint und jedenfalls schon im frühesten Beginn des Wirbelthierlebens als specifisch

functionelles Organ auftritt." Both these conclusions go too far in reading highly developed structures back into a primitive brain. The present paper shows that the cerebellum of *Petromyzon* is far from being a full equivalent of the cerebellum even of other fishes. The structure of the brain of *Petromyzon*, so far from indicating that the cerebellum is one of the oldest brain centers, shows quite the reverse; namely, that the cerebellum with the functions and relations characteristic of that organ in higher vertebrates, is scarcely represented at all in *Petromyzon* and is but poorly developed in any of the fishes. JOHANNES MÜLLER was much nearer the truth in pointing to the acusticum as the representative of the cerebellum of other fishes, for the cerebellum in *Petromyzon* is little more than the fused front end of the special cutaneous part of the dorsal horn of the medulla.

This interpretation readily explains SCHAPER'S ('99 b) difficulty in finding a caudal limit to the cerebellum in fishes. The cerebellum being the direct continuation of the acusticum, it has no sharp caudal limit.

HOUSER ('01) describes in *Mustelus* a general cutaneous nucleus and acusticum clearly separated by a deep groove. Both contain PURKINJE and molecular cells comparable with those in the cerebellum, and both are covered superficially by the cerebellar crest. He considers the general cutaneous nucleus as the direct continuation of the dorsal horn of the cord and the acusticum as a later derivative of the general cutaneous nucleus. The cerebellum has arisen as a fused outgrowth of the acustica. The PURKINJE cells are poorly developed as compared with those of *Acipenser* and seem to show similar gradations between the general cutaneous nucleus, acusticum, and cerebellum.

The medulla of *Mustelus* as described by HOUSER presents some unexpected peculiarities: the large size of the general cutaneous nucleus as compared with the acusticum, the absence of a lobus lineae lateralis above the acusticum, the presence of PURKINJE cells in the general cutaneous nucleus and the extension of the cerebellar crest over this nucleus as well as the

acusticum, and the entrance of sensory fibers into the acusticum only through a narrow neck between the cerebellar crest and the ventricle. These peculiarities together with the general appearance of the structures concerned, as far as they can be made out from HOUSER's few figures, have led me to think that HOUSER has given the name "general cutaneous nucleus" to the body which has been known to other authors as the tuberculum acusticum, and has given this latter name to the structure usually known as the lobus trigemini of selachians and ganoids (my lobus lineae lateralis). HOUSER makes no mention of this latter lobe, although its presence has been indicated by STANNIUS ('49) in *Raja*, *Spinax*, *Carcharias*; by GEGENBAUR ('71) in *Hexanchus*; by JACKSON and CLARKE ('76) in *Echinorhinus*; and by EWART ('89) in *Laemargus*. The general relations of the body which HOUSER calls the tuberculum acusticum, as far as they are shown in his Figs. 1 and 2, closely correspond to those of the lobus lineae lateralis in *Raja*, while all the sensory structures resemble those in *Acipenser*. If the names which I have suggested are applied to these structures, the peculiarities noted above no longer require explanation. Some other considerations also point to this interpretation. It was suggested by GORONOWITSCH ('88) and again by KINGSBURY ('97) that the position of the cerebellar crest in ganoids, between the acusticum and the lobus lineae lateralis, is to be explained by supposing that there has been a longitudinal infolding along the line of the crest resulting in turning the dendrites of the PURKINJE cells which originally were directed toward the outer surface, toward each other from the acusticum and lobus respectively. This suggestion is the most obvious and plausible explanation of the position of the PURKINJE cells in *Acipenser* and it finds beautiful confirmation in the brain of *Mustelus* as represented by HOUSER in his Fig. 2. Here the cerebellar crest covers the outer surface of the lobus lineae lateralis and acusticum (HOUSER's *t. a.* and *g. c. n.* respectively) and the lateral surface is deeply infolded so as to form a partly fused molecular mass like that in *Acipenser* between the acusticum and lobus lineae lateralis, which are almost completely separated in both

Acipenser and Mustelus. The PURKINJE cells, according to HOUSER's statement, have the dendrites directed toward the external surface; if so, those lying on either side of the deep groove must be directed toward one another as in Acipenser (cf. HOUSER's Fig. 2 with my figures in '98 b). This explanation of the position of the acusticum, lobus lineae lateralis, and cerebellar crest in selachians and ganoids is rendered entirely clear when the brain of Petromyzon is taken into account, where the lobus is seen to be only a special collection of cells in the dorsal part of the acusticum and the cerebellar crest covers the outer surface of the acusticum as the molecular layer of the cerebellum covers the granular layer.

The direct continuity of the *g. c. n.* with the dorsal horn, the ending of general cutaneous fibers in it, and the structure of the nucleus itself all agree with the tuberculum acusticum in Acipenser and Petromyzon. HOUSER, indeed, says that "JOHNSTON ('98 b) appears to include a part of this region under his *tuberculum acusticum*" (p. 95). In describing the tuberculum acusticum he says: "The term *trigeminal lobe* has been so variously used that it should be dropped from our nomenclature. The earlier writers on the brain of the selachian so designated the tuberculum acusticum" etc. (p. 100). From this it appears that HOUSER has consciously adopted new names for both these structures. The reason for this is not given, but it must lie in his conclusions regarding the central endings of the general and special cutaneous nerves. He represents the trigeminus alone as ending in the so-called general cutaneous nucleus, while the acustico-lateral fibers all enter his tuberculum acusticum through the narrow neck between the cerebellar crest and the ventricle (see his Fig. 2). In Acipenser and Petromyzon the large special cutaneous nerves plunge directly into the body of what HOUSER calls the general cutaneous nucleus and the bundles of fibers running forward and backward in that center and the endings of fibers are readily made out. HOUSER does not describe the point of entrance of any of these nerves, but says that they reach the acusticum as arcuate fibers from the opposite side. From this it seems probable that he has not

traced the fibers from their roots to the central endings. As I have described in detail for *Acipenser* ('01 c, p. 26-27 of the reprint) both direct root fibers and arcuate fibers pass through the narrow neck mentioned above. The same thing is probably true in *Mustelus*, since the correspondence in other particulars is so complete. HOUSER has failed to follow the root fibers through his general cutaneous nucleus. Aside from this difference in our results, there is a very great improbability in HOUSER's description, arising from the relative size of the parts concerned. HOUSER assigns the whole of his very large general cutaneous nucleus to a part of the trigeminus, the spinal V portion of that nerve going to the enlarged anterior end of the dorsal horn; while only the much smaller tuberculum acusticum serves as the place of ending of the great acustico-lateral system, except those fibers which go to the cerebellum. Even these latter pass through the acusticum. In other fishes both the V and the acustico-lateral fibers pass through or end in the body which he calls the general cutaneous nucleus.

These criticisms, however, do not in any way discredit the admirably clear and accurate account of the nerve elements in these and other parts of the brain. There is a remarkable agreement in the structure of the cutaneous sensory centers in *Mustelus*, *Acipenser*, and *Petromyzon* and the results of HOUSER's work give in general a very strong confirmation of my conclusions on the origin of the acusticum and cerebellum and their relation to the dorsal horn of the cord.

The use of the term *general cutaneous nucleus*, suggested by HOUSER, does not seem to the writer admissable, for the reason that the general cutaneous fibers do not end in any one nucleus or set of nuclei to the exclusion of other fibers. The fibers of the trigeminus in fishes have endings in the nucleus funiculi, nucleus trigemini spinalis, acusticum, and cerebellum. The only one of these nuclei which is exclusively general cutaneous is the nucleus trigemini spinalis, but since this receives only the smaller part of the general cutaneous fibers it seems best to keep the term which indicates its relation to the spinal V tract.

The fasciculus communis system in *Petromyzon* presents in general the same relations as in *Acipenser*. It is much smaller than in *Acipenser*, cells of the II type have not been found, and the secondary tract is too small and diffuse to be traced. The small size of the system and the absence (or paucity) of II type cells must be regarded as primitive characters. The latter leads the writer to doubt whether the II type cells in the lobus vagi of *Acipenser* have the importance which has been attributed to them. In *Petromyzon* the cells are more primitive in their form and position than in *Acipenser*, and the communis center is not nearly so highly developed as the cutaneous centers. Compare Figs. 8 and 11.

The central connections between the cutaneous and visceral systems are, as the writer has shown ('01 c, p. 119, 126), *nil*. The study of the brain of *Petromyzon* supports in every particular the conclusions on this point drawn from the brain of *Acipenser*, and furnishes additional evidence owing to the greater development of the spinal portion of the communis system. *Petromyzon* is to be added to the list of lower vertebrates in which the median nucleus and cervical bundle of CAJAL have been described (cf. JOHNSTON '01 c, p. 126). It is to be noted that the cervical bundle is much larger and extends farther caudally than in any other vertebrate, while the median nucleus merges with the central grey matter immediately dorsal to the canal. It seems probable that the visceral center in the cord is larger in *Petromyzon* than in higher forms, and it is pretty well established for all vertebrates that this center is wholly distinct from the cutaneous center in the cord, lying mesial to the latter and bordering on the canal. This supports the view already stated independently by C. J. HERRICK ('99, p. 56-58) and the writer ('01 c, p. 127).

The fasciculus communis system includes fibers distributed to general visceral surfaces and fibers to end-buds both in the mouth and branchial cavities and on the outer surface of the body. The writer has suggested ('01 c, p. 127-129) that these buds have essentially the same function wherever situated, namely to test the chemical quality of the water with respect

to its fitness for respiration or the presence of food, and that therefore the communis fibers all have visceral or organic functions. A fact having an important bearing on this question not before noticed, is the relatively simple character—the low grade of development or differentiation—of the communis center. In all vertebrates the communis center is simpler in structure than the cutaneous center, and this difference is already very well marked in the lowest craniates. This simplicity of the center is a sure indication of simplicity in the end organs. It is scarcely conceivable that the communis center, with its simple structure, should receive fibers from such diverse structures as the lining of the alimentary canal (general visceral), end-buds in the mouth and pharynx (taste), and end-buds on the outer surface serving functions of cutaneous sensation (somatic sensory). If the end-buds on the surface of the body are somatic sensory in function it must be supposed that they give rise to reflexes of some sort connected with the external relations of the animal. These must be added to the considerable range of reflexes of a visceral character which must be mediated by the communis center and its motor connections,—reflexes concerned with the movements of the alimentary canal, the respiratory and masticatory movements, and secretory activities. It must certainly be expected that if this center also has a somatic sensory function it should show some such differentiation and complexity of structure as do the centers for general cutaneous, lateral line, and auditory organs. The general and special cutaneous organs do not represent so wide a range of sensory impulses as would be represented by the general visceral, taste bud, and external end-buds with somatic sensory functions. From these considerations together with those presented in the previous paper ('01c) the writer is fully convinced that the end buds will all prove to have visceral or organic functions. The writer also awaits with the greatest interest embryological investigations which shall determine whether the buds have originated in the entoderm and found their way out upon the surface of the head and body through the gill slits, mouth, hypophysis, or some such structure as the adhesive organ of *Amia*.

HOUSER ('01) describes in *Mustelus* a distinct fasciculus communis formed of root fibers of VII, IX, and X, which runs back into the cord. He does not mention a commissura infima HALLERI or a median nucleus. In the lobus vagi he finds only cells of the II type, which he thinks come into relation with the cells of the visceromotor nucleus. It seems probable that HOUSER has worked with imperfectly impregnated preparations, since cells of the I type giving rise to a longitudinal tract are present in teleosts, ganoids, and *Petromyzon*. The fact that cells of the II type are few or absent in *Petromyzon* shows that the I type cells and secondary vagus tract constitute the more fundamental part of the central apparatus for the fasciculus communis system. Moreover, the direct connection of II type cells of the sensory nucleus with the motor cells is not probable on general grounds. It is not possible that all the visceral reflexes should be carried on by so simple an apparatus as suggested by HOUSER (p. 90, 94).

The general result of the study of the sensory systems of *Petromyzon* is to add support to every one of the theoretical considerations brought forward in discussing the brain of *Acipenser*.

B. The Mid-, Tween, and Fore Brain.

The only paper on these regions of the *Petromyzon* brain based on work by modern methods is that by F. MAYER ('97). A discussion of this paper will lead to the chief questions which I wish to consider. It is to be regretted that the final paper of this author has not as yet appeared as the preliminary paper is so brief that, in the absence of illustrative figures, it is impossible to know the author's meaning in all cases. For the same reason it is impossible to criticize the author's work in detail. There are certain statements of MAYER'S which, in the opinion of the present writer, receive no confirmation from any work which has hitherto been done on the brain of lower vertebrates. These points can not be discussed at least until the complete paper appears, but they are enumerated here. They are: the existence of a tractus thalamo-olfactorius arising from cells of

the thalamus and hypothalamus and ending in the glomerular layer of the olfactory lobe; fibers in the basal bundle from the hypothalamus to the striatum proper; the existence of the so-called Stabkranz; a resemblance between the cells of the hypothalamus and those of the striatum; the absence of cells from the outer and middle layers of the tectum; the formation of the fasciculus longitudinalis posterior of fibers from the commissura posterior. The facts with regard to these points, as they are understood by the present writer, are stated in the descriptive part of this paper. The following statements of MAYER are also to be regarded as very doubtful in *Petromyzon*: that the striatum sends fibers to the hind brain and hypothalamus; that the vertical cells in the tectum send fibers to the hind brain and the bipolar cells to the "cortex;" that the tectum sends fibers to the posterior commissure.

Some of these errors (as the writer must consider them) are due to, or at least connected with, the misinterpretation of the several parts of the fore brain. MAYER seems to have confused the nucleus thæniæ with the striatum, either describing the former nucleus alone as the striatum or including both in his description. This accounts for the statement that the cells of the hypothalamus resemble those of the striatum and that the latter have central processes and dendrites which are always directed backward. The cells of the nucleus thæniæ have those characters, those of the striatum for the most part do not. From his plate, however, it would appear that it is the ventral part of the lateral expansion to which the name "Basalganglion" is given. This is an error to the opposite extreme, since the striatum does not extend far laterally in the so-called hemisphere. The epistriatum seems to have been wholly overlooked by MAYER. AHLBORN stated that the thalamus extends forward to the anterior commissure at the cephalic limit of the lamina terminalis. This is the olfactory commissure of the present paper, and the thick dorsal portion of the wall of the fore brain which AHLBORN thus included in the thalamus has been shown above to be the epistriatum. MAYER seems to have completely ignored this important and prominent body. I was at first in-

clined to think that it was this body to which MAYER gave the name of "Hirnrinde," and so treated it in a paper read before the Baltimore meeting of the American Society of Morphologists ('01 b). It seems to me now that it is the dorsal portion of the lateral expansion which MAYER considers to be the cortex. If so, he has wholly disregarded the epistriatum! My mistake in understanding MAYER's description was due to the fact that it did not seem possible for anyone to overlook so large and conspicuous a body with so characteristic a structure as the epistriatum. Moreover, the cells of the epistriatum might be called pyramidal cells, while none in the dorsal part of the lateral expansion have any resemblance to pyramidal cells. This latter fact, together with the relations of the fiber tracts to and from this part of the fore brain show that it is not at all a cortex, but merely the area olfactoria. Since this is MAYER's own description of this center, he has precluded the possibility of applying to it the name *cortex*. The use of such terms as olfacto-corticalis, cortico-habenularis, etc., are therefore inadmissible.

Certain other statements made by this author deserve somewhat more detailed examination. He includes certain giant cells, which give rise to MÜLLERIAN fibers, in the grey matter of the "corpora quadrigemina" for no apparent reason. The cells lie in the central grey of the lateral and ventral wall of the mid brain. He states that the greater part of the posterior commissure is formed of fibers from the tectum destined to constitute the fasciculus longitudinalis posterior. In fact very few fibers from the tectum enter the posterior commissure, and the suggestion that the fasciculus is formed of fibers from either the tectum or posterior commissure can not be entertained for a moment, in the light of the origin of this fasciculus in other vertebrates from cells in the thalamus and from motor cells situated along the route of the fasciculus in the base of the brain. The fibers from the epiphysis to the posterior commissure can not exist in *Lampetra* and must be regarded as very doubtful from the fact that in known cases the fibers from the epiphysis enter the ganglia habenulae. The curious suggestion that

the giant MÜLLERIAN cells of the mid brain be considered as equivalent to KÖLLIKER's nucleus of the posterior commissure, because according to MAYER they send their dendrites through that commissure, requires no other comment than that the true homologue of KÖLLIKER's nucleus is present in *Lamprolaima*. The commissura transversa is constituted, according to MAYER, of his Stabkranz and of the dendrites of cells of the tectum. The latter are *at least* doubtful and I have (above) denied the existence of the Stabkranz in *Petromyzon* for the double reason that I have found no such fibers and that in the absence of a true cortex there can be no true Stabkranz;—and fibers running from the hind brain, tectum, and hypothalamus to the olfactory area are too anomalous to be considered. MAYER seems to have overlooked the large tractus lobo-bulbaris which constitutes the post-optic decussation. Instead of this he describes the fibers from the cells in the cephalic part of the hypothalamus as running to the striatum and olfactory area ("cortex"), partly crossed in the anterior and infundibular commissures. These, too, are unlike anything in the fish brain, and it would be difficult to state what their function would be. His description of fibers from the striatum to the hypothalamus and hind brain is due to confusing the nucleus thæniæ with the striatum. Fibers from the nucleus thæniæ do go to the hypothalamus. Fibers from the striatum end for the most part, at least, in the thalamus; I have been unable to demonstrate any going to the hind brain. It is not clear in the absence of figures, what MAYER means by the statement that there are no nerve cells other than mitral cells in the olfactory lobe,—whether he considers all the cells as mitral cells or denies the nervous nature of all except those lying near the glomeruli.

a. The olfactory lobe.

In the olfactory lobe of *Acipenser* the writer has described, besides true mitral cells, numerous slightly differentiated cells which come into relation with olfactory fibers in the glomeruli and send their neurites to the fore brain with those from the mitral cells. These cells were interpreted as corresponding to the "kleine Pinselzellen" and granules of higher vertebrates and it was

shown that even those cells which most resemble the granules had neurites. The explanation of this condition was that the lobe in *Acipenser* is relatively primitive and that these slightly differentiated cells are the material from which the highly differentiated elements of the higher olfactory lobe have developed. This was supported by reference to the lobe of *Rana* and of reptiles, in which similar cells are found ('01 c, p. 90, 172).

The olfactory lobe in *Petromyzon* gives the fullest confirmation of this interpretation. The existence of numerous cells at all levels of the olfactory lobe which are in relation with olfactory fibers in the glomeruli, the grade of differentiation of these cells being still lower than in *Acipenser*, the presence of somewhat larger cells near the glomeruli with the characteristics of mitral cells poorly developed, and the common destination of the neurites of all these cells give conclusive evidence that the olfactory lobe in the fishes is in the condition of a mass of slightly differentiated cells, from which the true mitral cells are the first to become differentiated. Later appear the small and superficial "Pinselzellen." It seems certain also that the granules are represented by the stellate, spindle, and granule cells, which are functional nerve cells in the fish, amphibian, and reptilian (?) brain.

b. The fore brain.

The identification of the parts of the fore brain with their characteristic connections brings *Petromyzon* into line with other fishes and, taken with similar findings in other parts of the brain, goes to show that the fundamental or reflex apparatus is already well developed in the ancestors of existing fishes. Probably very little of the mid, 'tween, and fore brain structure exists in *Amphioxus*, indicating the very great gap between the points at which *Amphioxus* and *Petromyzon* branched off from the phyletic tree. The somewhat complete development of the reflex apparatus, including the olfactory area, striatum, and epistriatum of the fore brain, in *Petromyzon*, does not at all warrant, however, the tendency shown by F. MAYER and others to read back into this primitive brain much of the complexity of the higher vertebrate brain. The result of this ten-

dency is seen in the recognition of a cerebral cortex with several appropriate tracts where nothing of the sort exists. Aside from a predisposition to find these structures, there is a certain suggestion of their presence to be found in the gross structure of the Petromyzon brain. This consists in the presence of lateral expansions of the fore brain containing cavities analogous in position to the lateral ventricles of higher vertebrates. Upon the dorsal wall of these apparent lateral ventricles, then, MAYER ('97) and STUDNICKA ('98) have found a so-called cortex. The proof that this is in no sense a true cortex, given in this and the previous paper ('01 a), makes it necessary to find some other explanation for the "lateral ventricles." As already suggested (p. 39), these are probably due to simple mechanical agencies. The displacement of the hypophysis and olfactory pit upon the dorsal surface of the head by the growth of the oral funnel is well known. That this organ has at the same time compressed and altered the form of the brain is not so evident, but a little attention shows it to be very probable. The olfactory pit is closely pressed against the olfactory lobe, so that the olfactory nerve is of no appreciable length. The lobe itself is short and wide and in surface view does not appear to be so distinctly paired as in other fishes. Internal examination shows, however, that the two lobes are widely separated throughout the greater part of their length by structures of very different nature,—dorsally by the epistriatum, ventrally by the lamina terminalis. The lamina contains the anterior commissure as usual, except that here it is divided into two distinct commissures, the cephalic one of which is related to the olfactory lobes alone and is situated near the cephalic end of the lobes. These facts indicate that the olfactory lobes have been compressed and pushed backward and outward by pressure from the olfactory pit. This has brought the lobes to lie at the sides of the axial portion of the fore brain and they have in turn crowded the olfactory areas outward and backward until they form the great lateral expansions to which the name "hemispheres" has been erroneously given. The whole fore brain at the same time has been somewhat bent upward as is indicated by the position of

the lamina terminalis. The chief effect of the pressure has been to produce a lateral bulging, and in this the cavity has participated. The form of the lateral cavities is readily explained by this alone. The cephalic horn is the cavity of the olfactory lobe in its usual relations; the caudal horn is the cavity of the fore brain carried outward and backward by the bending of its wall. The lateral bulging of the wall has resulted in a partial separation of the striatum and epistriatum, the epistriatum extending forward above the lateral cavity.

HOUSER notes the presence of spiny gemmules on the dendrites of striatum cells in *Mustelus* and suggests that they are characteristic of these cells in fishes, citing VAN GEHUCHTEN ('94) and JOHNSTON ('98 a) in evidence. In my later paper ('01 c) it was stated that the striatum cells are usually devoid of these gemmules and that they are characteristic of the epistriatum cells. I am convinced that it is exceptional for the striatum cells to bear spines in *Acipenser* and they never do in *Petromyzon*. It should be noticed further that VAN GEHUCHTEN probably saw only the epistriatum cells and erroneously supposed that their neurites joined the basal bundle.

c. The 'tween brain.

The comparative simplicity of the 'tween brain is one of the most marked characteristics of the brain of *Petromyzon*. Although the ganglia habenulae and epiphysis are large and apparently more important than in *Acipenser*, the remainder of the 'tween brain shows less differentiation. The nucleus anterior is not to be recognized and the central grey is more completely a nucleus diffusus than in other fishes, while in the hypothalamus the inferior lobes and corpus mammillare show too little differentiation to be considered separate centers. A large part of the cells of the central grey of the thalamus and mid brain send their neurites through the posterior commissure and constitute a nucleus homologous with that described by KÖLLIKER in mammals. The saccus corresponds in structure and relations so far as studied, with that of *Acipenser*.

d. The tectum.

The tectum has been shown to be more simple than in

Acipenser, especially as regards those elements which are in relation with the optic fibers. The question suggest itself, is the tectum relatively primitive or reduced, undeveloped or degenerated? The fact that the paired eyes present undoubted primitive characters indicates that the tectum is primitive. This accords with the description of the morphology of the cells related to the optic fibers. The writer hopes soon to investigate the brain of *Bdellostoma* with reference to this point.

NOTE—The paper of SCOTT ('87) on the development of *Petromyzon* escaped my attention when this paper was being written. As it contains several items of interest, a note is inserted here in the proof. SCOTT describes and figures the part played by the growth of the upper lip in carrying the olfactory pit up on the dorsal surface of the head. During this process, he says, the cerebral flexure partly corrects itself by rotation about a transverse axis through the mid brain. That this straightening of the brain is due to the pressure from the upper lip is not stated by SCOTT, but seems probable. This, together with the telescoping movement of the fore brain suggested in the present paper will account for the definitive form.

SCOTT has not traced the course of development of the body which he calls the second epiphysial vesicle (paraphysis of RETZIUS *et al.*), but he states in his summary that it is derived from the first vesicle (epiphysis) and comes into close relation with the left ganglion habenulae. The latter ganglion, in larvae of 12–25 millimeters, elongates and divides into two parts. The anterior part, perhaps during metamorphosis, becomes closely associated with the lower pineal vesicle and connected with the left ganglion habenulae by a fiber tract. This account of the origin of the mass of cells in the lower wall of the so-called paraphysis leaves no doubt as to their nervous character, but it throws no light upon the origin and homology of the vesicle itself. It is altogether probable that this is not a true paraphysis, since the paraphysis is a fold of the choroid plexus. Further investigation of the morphology, histology, and physiology of this region in *Petromyzon* is much needed.

SCOTT also states that the N. lateralis develops by a progressive differentiation of the ectoblast, with which the account of v. KUPFFER is in agreement.

C. *Primitive Characters in the Petromyzon Brain.*

The brain of *Petromyzon* shows its primitive character least in the general relations of its chief centers and fiber tracts and most in the characters of its nerve elements and the fine structure of the various centers. In the former regard this brain is much like the characteristic fish brain; in the latter respects it shows great peculiarities. In the fine structure of many parts of the brain there is a marked simplicity as compared with the

brains of other fishes, and in some cases this amounts to almost a complete absence of differentiation among the elements constituting the center. This simplicity is especially evident in the cerebellum, lobus vagi, tectum, hypothalamus, lobus olfactorius, as described in the foregoing pages.

Aside from this simplicity of nerve centers viewed from the standpoint of function, or considered as apparatus, many parts of the brain show primitive or embryonic characteristics in the form and position of the individual cells. In lower vertebrate brains the cells are commonly aggregated near the central cavities and the outer zone is chiefly made up of dendrites and fiber tracts. This is true to a greater degree of the brains of embryos or very young specimens. When these aggregations of cells are examined they are found in embryos to be masses of similar cells with slight differentiation; and in adults the greatest differentiation, as indicated by marked structural characters, is usually found in those cells which are farthest removed from the central aggregations. In this respect the brain of *Petromyzon* is to be compared with the embryo rather than with the adult, although the higher differentiation of the cells farther from the cavity is well illustrated.

The cells of the most primitive form stand near the central cavity, sometimes between the ependymal cells, and have a central process which extends down in the ependyma and helps to line the internal surface of the brain. There are no basal dendrites and only one peripheral dendrite which shows few and simple branches extending toward the surface through the fiber zone. The neurite arises from the dendrite or one of its chief branches. Such cells are found in *Petromyzon* in the corpus mammillare, where they constitute the whole of the grey matter; and in the acusticum, lobus vagi, cerebellum, central grey of the thalamus and mid brain, tectum, inferior lobes, nucleus thæniæ, striatum, and olfactory lobes, where they constitute a more or less important part of the structure. Such cells are always relatively small and they are most numerous in those parts of the brain which have not reached a large growth.

The study of the cells in the brain of *Acipenser* and *Pe-*

tromyzon shows that growth and differentiations of cells in the various centers takes place by several kinds of changes, of which the following are chief:

- (1) Migration farther from the central cavity.
- (2) Elongation of the central process, followed by its loss or modification into a dendrite.
- (3) Growth in volume of the cell body and dendrites.
- (4) Increasing complexity of the dendritic branching and of the number of dendrites given off from the cell body, with a tendency in the more highly developed centers to a specialization in the form and arrangement of the dendrites.
- (5) A tendency in slightly differentiated centers for the disposition of the dendrites to be determined by the direction of the fiber tracts among which they lie.

The migration of the cell with consequent elongation of the central process is beautifully illustrated in the inferior lobes of *Petromyzon*, and in the nucleus thaeinae of *Acipenser*. The latter case also illustrates the modification of the central process into a dendrite, the cell body in this especial case becoming bipolar with two long dendrites ('OI c, Fig. N). The bipolar cells of the tectum of *Petromyzon* probably have a similar history. In both these cases the neurite is given off from the end or near the end of the original (peripheral) dendrite. The growth and increase in number of dendrites is accompanied in some cases by migration of the cell body, and in some cases not. In the former case the cells frequently become multipolar or stellate, passing through numerous intermediate gradations, as in the tectum and olfactory lobe of both *Acipenser* and *Petromyzon*. In the latter case the cells are likely to become spindle shaped or pyramidal with few or small basal processes and with the peripheral processes greatly developed in special forms, as in the vertical cells of the tectum in *Acipenser* and in the epi-striatum cells in both *Acipenser* and *Petromyzon*. Finally, it is very noticeable in those centers, such as the tectum and olfactory lobe, in which occur central grey masses with cells scattered in the peripheral fiber zone, that the cell is more highly developed the further it is removed from the central cavity. By

development it is meant to include size and complexity together with the disposition of the dendrites with reference to functional efficiency. For example: the functional efficiency of a stellate cell in the tectum and of an epistriatum cell may be equally great, although the latter has developed along special lines and has not always migrated from the central cavity; but the efficiency of either of these is much greater than that of the cells with central processes and poorly developed dendrites in any center.

It occasionally happens that cells are found holding the same relations to the external surface of the brain as the cells of the central grey hold to the cavity. Examples of this are found in the superficial horizontal and other superficial cells in the tectum of *Acipenser* and *Petromyzon*. In these cases the same principles hold, since these cells were primitively in contact with the external surface. In the case of the superficial cells of the fore brain which constitute the cortex (e. g., in *Acipenser*) it is a question whether they have undergone further changes than any of those above described, or are to be compared with the primitively superficial cells of the tectum.

It would appear from a comparative view of the choroid plexuses in the roof of the brain that they are more extensive in the lower forms. In *Petromyzon* the dorsal wall is non-nervous throughout its whole extent except where commissures occur, and it is only in the cerebellum that the commissure is accompanied by a thick wall of cells in the median line. The primitive vertebrate brain seems to have had a choroid roof throughout its whole extent except for the commissures.

V. SUMMARY OF RESULTS.

The study of the brain of *Petromyzon* has brought out the following new facts and theoretical conclusions:

1. The visceromotor and somatic motor nuclei of the medulla are imperfectly differentiated.

2. The MÜLLERIAN fibers are the neurites of giant cells lying in the central grey (ventral and lateral motor columns) of the medulla and mid brain which have the same general characters

as motor cells. They do not arise from the spindle cells of the acusticum and do not decussate.

3. The nucleus funiculi is diffuse, but recognizable as a special nucleus.

4. The nucleus funiculi is continuous cephalad with both the nucleus trigemini spinalis and the tuberculum acusticum. Those together represent the acusticum in *Acipenser*.

5. The acusticum is covered externally by a cerebellar crest as in selachians and ganoids.

6. The acusticum and cerebellar crest are continuous with the granular and molecular layers of the cerebellum, respectively.

7. There is a lobus lineae lateralis homologous with that of *Acipenser* and selachians. In *Petromyzon* it is evident that this lobe is essentially a part of the acusticum.

8. The nucleus funiculi, nucleus trigemini spinalis (?), acusticum, and cerebellum have in common two chief types of cells which are characteristic of these centers in fishes and of the cerebellum in higher forms: namely, large cells which are either PURKINJE cells or the forerunners of PURKINJE cells, and granule cells.

9. The VIII root fibers end in the cerebellum, acusticum, and nucleus funiculi; those of the lateral line VII end in the cerebellum and acusticum; those of the V in the cerebellum, acusticum (?), nucleus trigemini spinalis, and nucleus funiculi.

10. The presence of lateral line organs is confirmed. These are numerous pit organs arranged much as in other fishes, and the special cutaneous center in the medulla is correspondingly large.

11. There is a large post-auditory lateral line root which forms the greater part of the lateral line nerve and gives a component to the trunk of IX.

12. The VII-X anastomosis is composed almost exclusively of lateral line components. It receives a few communis fibers whose destination is unknown.

13. The N. lateralis is a true lateral line nerve, receiving

its fibers from the VII-X anastomosis and the post-auditory lateral line root.

14. The lateral line organs are innervated by components which find their central endings in the acusticum and cerebellum.

15. The cerebellum is very poorly developed. Fibers from the lobi inferiores are the only ones which enter it from in front.

16. The PURKINJE cells are very slightly developed in the cerebellum and correspond closely to the large cells in the acusticum. They send their neurites as internal arcuate fibers to the tectum.

17. The spindle cells in the acusticum have club-like endings of VIII and lateral line VII fibers closely applied to them. The cells do not give rise to MÜLLERIAN fibers, but their neurites go as internal arcuate fibers to the tectum.

18. The above facts give the strongest support to the idea of the morphological unity of the acusticum and cerebellum with the nucleus trigemini spinalis and the dorsal horn of the cord. All the cutaneous centers (end-bud center excepted) have been developed from a common *Anlage* which is the direct continuation and equivalent of the dorsal horn of the cord.

19. The presence of simple sense organs corresponding to the end-buds of other fishes is confirmed.

20. These are not very numerous and the fasciculus communis system is correspondingly small.

21. There is a fasciculus communis VII root which has the same relations as in other fishes.

22. The fasciculus communis has a commissura infima HALLERI, a median nucleus, and a large cervical bundle. These structures are probably constant in all vertebrates.

23. The communis center is simpler in structure than in *Acipenser*. The essential elements seem to be cells of the I type which give rise to a secondary vagus tract.

24. The tectum opticum presents a much lower grade of differentiation than in other fishes owing to the poor development of the eyes. The cells serving as a secondary somatic center are similar to those of *Acipenser*.

25. The tracts which enter and leave the tectum correspond closely to those in *Acipenser*, except that there is no tract to the cerebellum. All the tracts have a somewhat more simple arrangement than in *Acipenser*.

26. A large part of the cells of the central grey of the mid- and 'tween-brain constitute the nucleus of the posterior commissure, homologous with the nucleus described by KÖLLIKER in mammals. The fibers of the commissure are destined to the medulla.

27. The ganglia habenulae and bundles of MEYNERT correspond in all important features to those of *Acipenser*, except that the right bundles contain ascending fibers which end in the right ganglion.

28. The pineal apparatus probably functions as a light percipient organ, it is in relation with the left ganglion habenulae only.

29. The hypothalamus is less highly differentiated than in *Acipenser*. Its tracts correspond in general with those of the hypothalamus of *Acipenser*.

30. There is a centrifugal tract to the saccus vasculosus which has the same relations as in *Acipenser*.

31. The tractus lobo-epistriaticus crosses in the post-optic decussation instead of the anterior commissure.

32. The form of the fore-brain has become greatly modified by pressure from the buccal apparatus. The striatum occupies the base, the epistriatum the dorsal part of the lateral wall. The olfactory lobes and areas have been telescoped backward and to the sides of the striatum and epistriatum. This has led to modifications of the cavity which give the appearance of lateral ventricles.

33. The epistriatum is an olfactory nucleus and sends short neurites into the striatum; it also forms part of a coordinating apparatus for impulses coming from the tectum by way of the hypothalamus.

34. The olfactory area, which constitutes the great lateral expansion, receives fibers from the olfactory lobe and sends its

neurites to the hypothalamus and ganglion habenulae as in other fishes.

35. The nucleus thaeinae sends its neurites to the same destinations.

36. There is no cortex.

37. The olfactory lobe has a large number of slightly differentiated cells which receive and transmit olfactory impulses. The mitral cells are few in number and very poorly developed.

38. The brain shows marked primitive characters in certain centers and especially in the morphology and disposition of its individual nerve elements.

39. This brain offers considerable evidence that brain cells are primitively epithelial in character and that they increase their complexity of form and their functional efficiency as they become removed from the central cavity (or the external surface).

40. The conditions in *Petromyzon* suggest that the primitive vertebrate brain had a complete choroid roof for its whole length, thickened only by commissures.

Morgantown, W. Va.

October 16, 1901.

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DESCRIPTION OF FIGURES.

ABBREVIATIONS.

- ac.*—tuberculum acusticum.
ac. dm.—dorso-median nucleus of the acusticum.
ac. vl.—ventro-lateral nucleus of the acusticum.
a. o.—area olfactoria.
aq.—aqueduct of Sylvius.
au. c.—auditory capsule.
b. M.—bundle of Meynert.
c.—cerebellum.
c. a.—commissura anterior.
c. ans.—commissura ansulata.
c. c.—cerebellar crest.
c. com.—cerebellar commissure.
c. g.—central grey.
ch. ll.—optic chiasma.
c. m. corpus mammillare

- c. o.*—commissura olfactoria.
- c. p.*—commissura posterior.
- ch.*—chiasma of the optic nerve.
- ch. s.*—chorda sheath.
- c. i. H.*—commissura infima Halleri.
- com. c.*—commissural cells in the medulla.
- c. s.*—commissura superior.
- d.*—dermis.
- d. b. M.*—decussation of the bundles of Meynert.
- d. III.*—decussation of III nerve.
- d. h.*—dorsal horn.
- d. p.*—decussatio postoptica.
- e.*—epistriatum.
- epid.*—epidermis.
- ep.*—epiphysis.
- f. b. ven.*—fore brain ventricle.
- f. l. p.*—fasciculus longitudinalis posterior.
- f. c.*—fasciculus communis.
- g. l.*—granular layer of cerebellum.
- g. h.*—ganglia habenulae.
- gr.*—granule cells of cerebellum.
- g. M.*—giant cells of Müllerian fibers.
- H. z.*—Hinterzellen.
- i. a.*—internal arcuate fibers.
- i. a. P.*—internal arcuate fibers from Purkinje cells.
- III.*—third ventricle and third nerve.
- IV.*—fourth ventricle and fourth nerve.
- l. i.*—lobus inferior.
- L. l. l.*—lobus lineae lateralis.
- l. l. VII.*—the lateral line VII nerve and root.
- l. l. X.*—postauditory lateral line root.
- l. m. c.*—lateral motor column.
- l. o.*—lobus olfactorius.
- l. t.*—lamina terminalis.
- l. v.*—lobus vagi.
- m.*—mitral cells.
- m. c.*—motor cells.
- M.*—Müllerian fibers.
- med.*—medulla.
- n. b. M.*—nucleus of the bundles of Meynert.
- n. III.*—nucleus of the third nerve.
- n. c. p.*—nucleus of the commissura posterior.
- n. f.*—nerve fibers; nucleus funiculi.
- n. l. l.*—the lateral line nerve.
- n. sp. V.*—nucleus trigemini spinalis.
- n. t., n. th.*—nucleus thaeniae.
- o.*—lower olive.
- o. p.*—olfactory pit.

- P.*—Purkinje cells.
p.—paraphysis.
pl. c.—choroid plexus.
R.—Reissner's fiber.
r. p.—recessus praeopticus.
r. po.—recessus postopticus.
s.—corpus striatum.
sac.—saccus vasculosus.
s. c.—sense cells.
s. f.—sensory fibers.
sp. c.—spindle cells.
sp. c. f.—neurites of spindle cells.
sp. V.—spinal V tract.
th.—thalamus.
t. o.—tectum opticum.
tr. b.-t.—tractus bulbo-tectalis.
tr. e.-s.—neurites of epistriatum cells.
tr. l.-b., tr. l.-b. + c.—tractus lobo-bulbaris et cerebellaris.
tr. m.-b.—tractus mammillo-bulbaris.
tr. o.-h.—tractus olfacto-habenularis.
tr. olf.—tractus olfactorius.
tr. op.—tractus opticus.
tr. s.-th.—tractus olfacto-lobaris.
tr. th.-e.—tractus lobo-epistriaticus.
tr. th.-sac.—tractus thalamo-saccus.
tr. t.-th.—tractus thaenia-thalamicus.
tr. t.-b.—tractus tecto-bulbaris.
tr. t.-l.—tractus tecto-lobaris.
v. m. c.—ventral motor column.
1m.—first motor spinal nerve.
1s.—first sensory spinal nerve.
2s.—second sensory spinal nerve.
V.—nerve called by AHLBORN the abducens.
VII.—the seventh nerve proper, i. e., fasciculus communis and motor roots.
VII-X.—anastomosis of pre- and post-auditory lateral line components.
IX, X.—the ninth and tenth nerve roots.

PLATE I.

Fig. 1. Lateral view of the brain magnified about 30 diameters. The roots of the cranial nerves are inserted diagrammatically from sections. The roots of VII and VIII appear a little too far caudad. From a specimen of which the whole head was hardened in 20 per cent. formol.

Fig. 2. Median sagittal section of the brain to show form of cavity and the position of commissures. The small figure to the right is a horizontal section of the inferior lobes.

Figs. 3-20. A series of transverse sections inclined forward in the plane of MEYNERT'S bundles. Owing to difference in curvature of different brains it

is impossible to indicate the position of all of the sections accurately in such drawings as Fig. 1 or Fig. 30. For example, in the brain from which this series of sections was made the fore brain is curved upward much more than in that of Fig. 1, so that a line through the optic chiasma and the lower part of the olfactory commissure is parallel with the bundles of MEYNERT. The drawings were made at a magnification of 120 diameters and are reduced to 40 diameters. The nerve elements shown are all drawn directly from the sections outlined, except in a few cases where elements are borrowed from corresponding sections of another series in the same plane. No attempt has been made to render the sections diagrammatically complete.

Fig. 3. Through the second sensory spinal nerve.

Fig. 4. Through the first motor spinal nerve.

Fig. 5. Through the first sensory spinal nerve.

Fig. 6. Through the hypoglossus.

Fig. 7. Between XII and the last root of X.

PLATE II.

Fig. 8. Through the third root of X.

Fig. 9. Through the sensory IX. On the outer surface of the nucleus funiculi is shown diagrammatically the common plate of cells from which the nucleus trigemini spinalis and the acusticum differentiate.

Fig. 9 a. A vertical transverse section through a point between the planes of Figs. 9 and 10. Iron haematoxylin. To show relative position of the sensory centers.

Fig. 10. Through the lateral line X nerve and the motor IX.

Fig. 11. Through the caudal part of the VII-VIII root complex.

Fig. 11 a. Vertical transverse section through the VII-VIII roots. Iron haematoxylin.

PLATE III.

Fig. 12. Through the cephalic border of the dorsal lateral line VII root.

Fig. 13. Through the V nerve and the tectum.

Fig. 14. Through the tectum in front of the dorsal decussation, and through the decussation of the bundles of MEYNERT.

PLATE IV.

Fig. 15. Through the posterior commissure and the decussation of the bundles of MEYNERT.

Fig. 16. Through the ganglia habenulae and the bundles of MEYNERT.

Fig. 17. Through the superior commissure and the corpus mammillare.

PLATE V.

Fig. 17 a. Two vertical transverse sections between the planes of Figs. 17 and 18 to show the arrangement of the tractus thalamo-epistriaticus, tractus lobo-bulbaris, tractus olfacto-habenularis, etc. Iron haematoxylin. The right half of the drawing represents a section rostral to that shown in the left half. The tractus thalamo-epistriaticus is continued ventrally in Fig. 18, but is not labelled.

Fig. 18. Through the postoptic decussation, olfactory areas, and the epistriata.

Fig. 19. Through the optic chiasma, olfactory commissure and olfactory lobes.

Fig. 20. Through the olfactory lobes and the nucleus thæniæ.

PLATE VI.

Fig. 21. Transverse section of the lobus vagi and the nucleus funiculi at about the same level as that of *Fig. 7*.

Fig. 22, A and B. Sagittal sections of the cerebellum and of the hind and mid brain to show the PURKINJE cells and the course of their neurites. *B* is farther laterally than *A*, and the roots of V and VI are diagrammatically inserted from another section to show the fibers of V to the cerebellum. In *A* is shown at a higher magnification the part included between the small crosses in *B*.

Fig. 23. Three spindle cells lying close together in the lateral nucleus of the acusticum, near the cephalic end. The endings of the VIII fibers are shown in surface and profile.

Fig. 24. Root of the III nerve and adjacent structures. Iron hæmatoxylin. Transverse. At *a* is shown a part of the section immediately behind the decussation of III, to show how the cavity drops to the level of the spindle cell fibers. Compare *Fig. 2*. The nucleus of III is shown larger in the main figure than it really is. It is this large just in front of the decussation of the roots.

Fig. 25. One of the pyramidal cells from the surface of the tectum.

Fig. 26. An epistriatum cell in transverse section.

PLATE VII.

Fig. 27. Section of an end-bud from the dorso-lateral surface of the body in about the region of the second spinal nerve. \times about 730.

Fig. 28. The head of *Lampetra* in lateral and ventral views to show the distribution of the lateral line organs.

Fig. 28 a. Section of a lateral line organ. Only a few sense cells and two supporting cells are shown.

Fig. 29. Diagram of the sensory roots are seen from the side.

PLATE VIII.

Fig. 30. Diagram showing the approximate course and position of the chief fiber tracts. The brain is considered as a transparent body viewed from the side. In a general way the depth of the lateral tracts beneath the surface is shown by the shading, the deeper tracts being more heavily shaded, those near the cavity black. As in *Fig. 1*, the VII-VIII roots are placed too far caudally. The figure is rather a sketch than an accurate scheme, since the limitations of black and white reproduction make it impossible to show the several structures in their exact positions. The relationships are, however, truly indicated.

AN ATTEMPT TO DEFINE THE PRIMITIVE FUNCTIONAL DIVISIONS OF THE CENTRAL NERVOUS SYSTEM.

By J. B. JOHNSTON.

The time has come, as I think every comparative neurologist feels, that we must break away from the old cumbersome nomenclature and descriptions imposed by human anatomy, and create a new and simple mode of describing the brain which shall express rather than obscure the functions of its several parts. Any movement of this kind must be made with the greatest care regarding the foundation in fact and also with due care to avoid too great a gap between the old and the new. Although the contribution offered here is based chiefly on the author's investigation of the brain of fishes, full consideration has been given to the work of others, and many parts of the following scheme have been suggested by one or another of numerous investigators, of whom GASKELL, STRONG, and HERRICK may be named.

The analysis by STRONG (18) of the cranial nerves into components which serve similar peripheral organs and have the same central endings, has given both stimulus and direction to the most fruitful period in the study of the cranial nerves. This work, which has been extended by HERRICK (7, 8, 9), and others, has also helped toward a better understanding of the central system. The investigation of the sturgeon brain by the present writer (12) led to the discovery of no less definite and clearly marked divisions of the central system corresponding to the components of the cranial nerves. The study of the brain of *Petromyzon* (13) shows that it, too, falls strictly in line with the brain of other fishes in this regard. The work of HOUSER (10) on the selachian brain and the results of those students of the cranial nerves who have investigated the internal relations of the nerve components, are in accord with these results in

most respects. We may, therefore recognize certain *functional divisions* of the whole nervous system, and note that the successive parts of each division present a serial homology. A given functional division *consists of all the peripheral end-organs belonging to a given type, the nerve components which connect them with the brain, and the brain center in which these components end or take their origin.* Several such functional divisions, sensory and motor, constitute the reflex apparatus which governs the body. There are added to this on the one hand the specialized sympathetic system, and on the other hand the "higher brain centers" which serve for more complex interrelation and coördination, and in higher vertebrates for voluntary (conscious) activities. The scope of the present paper does not admit the

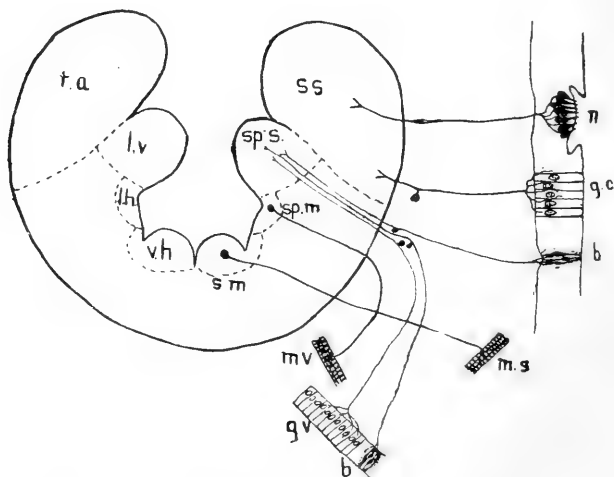


Fig. 1.—Diagram of the functional divisions in the region of the medulla. *b.*—end-buds; *g. c.*—general cutaneous components; *g. v.*—general splanchnic components; *l. h.*—lateral horn or nucleus ambiguus; *l. v.*—lobus vagi or fasciculus communis; *m. s.*—somatic musculature; *m. v.*—visceral musculature; *n.*—neuromasts; *s. m.*—somatic motor division; *sp. m.*—splanchnic motor division; *sp. s.*—splanchnic sensory division; *s. s.*—somatic sensory division; *t. a.*—tuberculum acusticum; *v. h.*—ventral horn.

discussion of the sympathetic system. It is proposed to compare the chief features of the functional divisions in the trunk and head regions, and to inquire briefly how far the brain itself

can be reduced (in lower vertebrates) to terms of these functional divisions as they are represented in the spinal cord and medulla oblongata.

The several functional divisions are present in the most complete form in the medulla and cranial nerves of fishes, and the following definition of them is taken from this region.

A. Afferent (sensory) divisions.

- a. Somatic sensory: stimuli received from the external environment; give rise to reflexes (locomotor or other) which directly affect (modify) the animal's relation to its environment (in man, commonly give rise to sensations and conscious reactions).
 1. General cutaneous sub-division; brain centers continuous with the dorsal horn of the cord and in part highly specialized as the centers of (2); fibers constituting components of the V, IX, and X roots and reaching their final distribution by way of various rami of the cranial nerves; innervating the skin without special sense organs (free nerve endings).
 2. Acustico-lateral sub-division: brain centers primitively identical with those of (1) but in part more highly specialized in all present vertebrates; fibers constituting the post- and pre-auditory lateral line roots and the root of VIII; innervating special sense organs in the skin which are genetically related (pit and canal organs, SAVI's vesicles, ampullæ of LORENZINI, and the ampullæ of the internal ear).
- b. Splanchnic sensory: stimuli received from the lining of the alimentary canal and from special organs in the branchial cavities, mouth, and on the surface of the head and body; give rise to reflexes which affect the organic activities (nutrition, respiration, circulation) and do not commonly produce sensations and voluntary movements.
 1. General splanchnic sub-division: brain centers continuous with the region of CLARKE's column of the

cord (afferent sympathetic center); fibers constituting the sensory VII, IX, and X roots exclusive of components above mentioned and (2) below, and reaching their final distribution by way of the visceral rami of the cranial nerves: innervating the general mucous surfaces. This sub-division in all vertebrates mediates only the vague "general" or "organic" feelings and seldom or never gives rise to immediate reflexes directed toward the environment.

2. End-bud sub-division: center and fibers not as yet distinguishable from those of (1); innervating taste buds in the mouth and end-buds in the branchial cavities and over the surface of the head and body. This sub-division serves especially the gustatory function, including testing the water with reference to its fitness for respiration. It gives rise to reflex movements of the visceral (lateral plate) musculature.

B. Efferent (motor, secretory) divisions.

- a. Somatic motor: brain centers corresponding to the ventral horn of the cord; fibers constituting the motor III, IV, VI, and XII nerves; innervating somatic musculature (from the mesoblastic somites).
- b. Splanchnic motor: brain center corresponding to the lateral horn of the cord; fibers constituting the motor V, VII, IX, and X nerves; innervating muscles of the branchial, hyoid, mandibular, and labial cartilage arches (derived from the lateral plates).

Thus the nervous system is analyzed into four great divisions, of which it may be said *in general* that the somatic sensory and somatic motor divisions act together in the external, animal activities of the organism; while the splanchnic sensory and motor divisions have to do with the internal and vegetative activities. The somatic divisions have to do with external, specific, localized, conscious sensations and with reflex or voluntary, conscious, movements in relation to external environment;

the splanchnic divisions have to do with the internal, vague, poorly localized, general sensations and with movements of the viscera related to the processes of nutrition, respiration, etc. So far as simple reflexes are concerned, it is probable that the somatic and splanchnic divisions remain independent. When stimuli received by either sensory division give rise, or seem to give rise, to reflexes in the other motor division, there has been an intervention of higher nerve centers or of stimuli from some other sense organ, such as the eye. An example of the latter is found in body movements for the purpose of catching food.

We pass now to the comparison of the several regions of the central nervous system with reference to the four functional divisions. In the trunk region there is found a relatively simple condition in which all four divisions are represented, as follows :

somatic sensory : dorsal horn of the cord, sensory fibers with general cutaneous distribution.

splanchnic sensory : region of CLARKE'S column, sensory fibers distributed to viscera by way of the dorsal roots and the sympathetic.

somatic motor : ventral horn, motor fibers supplying body musculature.

splanchnic motor : lateral horn, motor fibers to the viscera.

Associated with these four grey columns in the cord are fiber tracts which are not important, however, for the comparison with the brain. On the other hand, the commissural and tract cells, which give rise to the greater part of the longitudinal tracts of the cord, are of great importance for this comparison, as will appear below.

As the cord passes into the medulla each of the columns undergoes certain modifications due to the increase or reduction of the peripheral organs belonging to the same division. The somatic motor column gives rise to the nerve commonly known as the hypoglossus, which innervates tongue and tongue-shoulder-girdle musculature. This nerve is only a remnant composed of a variable number of ventral roots (3 to 8 in Gnathostomes)

out of about 11 original spino-occipital somatic motor nerves in primitive craniates (3). The disappearance of the musculature innervated by these nerves has led to an increasing reduction of the somatic motor column of this region in the ascending series of vertebrates. Rostral to this region represented by the hypoglossus, in which ventral nerves still appear in the ontogeny in fishes, a number of head segments represented by the branchial region have no somatic motor roots or center in craniates. Still further rostrally, however, somatic muscles are present in the form of eye muscles, and these are innervated by the VI, IV and III nerves, whose nuclei of origin in the medulla and base of the mid brain belong to the somatic motor column. The region in which this column is interrupted contains a tract of fibers, the fasciculus longitudinalis dorsalis,¹ formed by fibers from the somatic motor column which run for a short distance in this tract before going out in their nerves. This somatic motor fasciculus is continued rostrally beyond the nucleus of the III nerve into the thalamus, where its fibers take origin from the cells of a special nucleus. The presence of this nucleus and tract rostral to the first somatic motor nerve is probably connected with the former existence of a somatic motor nerve rostral to III. This nerve would probably correspond to the "anterior head cavity" of PLATT. The nucleus of the somatic motor fasciculus lies not far from the anterior end of the brain axis in the region of the chiasma, and the center for the somatic musculature would thus seem to have a greater extent than any of the other divisions.

The splanchnic motor column as it enters the medulla becomes rapidly enlarged, forming the nuclei of origin of the motor X, IX, VII, and V nerves, supplying the musculature of the branchial arches (nucleus ambiguus of the higher vertebrates). It occupies the same position here as in the cord, lateral to the ventral horn, and is distinguished from the somatic

¹ I propose that this tract be known hereafter as the *somatic motor fasciculus*. The present name indicates nothing as to its nature or function and gives only an erroneous impression as to its position. It is no more *longitudinal* than many other tracts, and is in no sense *dorsal*, but lies ventral to the central canal.

motor column with varying degrees of clearness in different fishes. In *Petromyzon* the two columns are distinct in position and have different histological characters. The same seems to be true in *Mustelus* (HOUSER). In *Acipenser*, on the other hand, only that part of the splanchnic motor column which is related to the V and VII nerves lies in a separate position lateral to the somatic column. There are, however, indications of a complete separation throughout the medulla, chief of which is the fact that the fibers of the motor VII, IX, and X nerves, which seem to come from the somatic motor fasciculus, in reality only run along the lateral side of that fasciculus and can be distinguished from it. The splanchnic motor nucleus ends quite abruptly with the nucleus of the motor V, although it primitively gave rise to one or more pairs of nerves rostral to V, of which the motor component of the ophthalmicus profundus V is still found in some cases in the ontogeny.

The somatic sensory division is in most Anamnia the largest of the four divisions in the head region and presents important modifications in its centers owing to the differentiation of its peripheral organs. In the trunk region the somatic sensory components of the dorsal roots belong to one system only, the general cutaneous. In the head region the presence of the various organs of the lateral line system and the ear has called forth the acustico-lateral system of nerves and, correlatively, great specialization in the somatic sensory centers in the hind brain. In consequence of these changes there are to be recognized two fairly distinct sub-divisions of the somatic sensory division, the general cutaneous and the acustico-lateral. The first of these seems on superficial examination to correspond fully to the somatic sensory division in the trunk, since it is continuous centrally with the dorsal horns and tracts of the cord and peripherally supplies general cutaneous fibers to the whole head. More careful examination of the central relations (12, 13) has shown, however, that the acustico-lateral centers have almost equally close relations with the somatic centers in the cord, that these relations are most intimate in the lowest forms studied, and that the progress of histological differentiation of the more

highly specialized acustico-lateral centers from the more simple general cutaneous centers can be traced in all its stages in the fishes. The lowest stage of histological development is found in the lowest form (*Petromyzon*). It will appear from what follows that the arrangement of the centers gives further evidence that they are sub-divisions and not separate divisions.

The general cutaneous components reach their distribution in various rami, innervating all the skin rostral to the innervation territory of the first free spinal nerve, except in those cases in which one or more dorsal roots of the spino-occipital nerves persist. Corresponding to this wide innervation territory, the general cutaneous centers have a great extent in the brain. They include the nucleus common to the dorsal tracts of the cord and the spinal V tract (all vertebrates); special collections of cells accompanying the latter tract (*Petromyzon*), or the tuberculum acusticum in the region of the X to V nerves (*Acipenser*), or both (*Mustelus*, 10); and the granular layer of the cerebellum (*Acipenser*, *Petromyzon*, *Scyllium* (2)). This wide central distribution of the general cutaneous fibers shows clearly that the whole extent of the somatic sensory centers in the brain originally belonged, and still belongs in part, to the general cutaneous system. In other words, the acustico-lateral system is an offspring of the general cutaneous system and the latter still claims the tuberculum acusticum and cerebellum as parts of its center. There is no particular "general cutaneous nucleus." The end-arborizations of the general cutaneous fibers lie mingled with those of the acustico-lateral components in each of the chief portions of the somatic sensory column of the brain. This does not mean that the two components have precisely the same central relations, since different connections may be set up by the neurites of the cells in the sensory nuclei. It is true, however, that the central relations of the general cutaneous and acustico-lateral components are so closely similar as to indicate that their centers are genetically related.

The acustico-lateral sub-division, although not separated centrally from the general cutaneous, is responsible for the great development and histological differentiation of the acusticum

and cerebellum. In all vertebrates a part of the fibers of this system, the spinal VIII tract, runs caudally parallel with the spinal V tract and ends in a special nucleus at the caudal end of the medulla. In fishes this nucleus is closely associated with (Acipenser) or forms an integral part of (Petromyzon) the common nucleus of the spinal V and dorsal tracts. In contrast to this, which indicates the close connection between the two subdivisions, stands the high degree of histological differentiation of the acusticum and cerebellum, which form the chief centers for the acustico-lateral components. The considerations regarding the origin and development of the cerebellum and its relation to the acusticum which have been urged by the writer (12, 13), have been quite fully confirmed by the results of HOUSER's work on *Mustelus*. The cerebellum contains the same types of cells as the acusticum, and the characteristic elements of the cerebellum, the PURKINJE cells, are present in the acusticum also and are developed from the ordinary large cells of the acusticum. The cerebellum is, therefore, a derivative of the rostral end of the acusticum. It may be said, then, that the somatic sensory division of the nervous system has a large center in the hind brain which is essentially a unit with the dorsal horn, but presents a remarkable degree of differentiation as compared with the dorsal horn. Almost all the stages of the development of the complex acusticum and cerebellum from the simple structure of the dorsal horn can be traced in the brain of existing fishes.

The splanchnic sensory division has its center in the cord in the region of CLARKE's column probably in all vertebrates. This conclusion rests on GASKELL's (4) experimental and theoretical considerations, on CAJAL's (1) study of the upper part of the cervical cord in young mammals, on ONUF and COLLINS' (15) experimental researches on the sympathetic in mammals, and upon the independent investigation of the transitional region between medulla and cord in lower vertebrates by HERRICK ((7) *Menidia*, *Mugil*) and the writer ((12) *Amia*, *Acipenser*, *Coregonus*, *Catostomus*, *Rana*; (13) *Petromyzon*). The fibers ending in this center come from the sympathetic system

by way of the dorsal roots. In the rostral portion of the spinal cord there appears a bundle of fibers, varying in size in different vertebrates, which lies dorsal to CLARKE's column and increases in size as it passes forward. The fibers of this bundle come from the roots of the X, IX, and VII nerves and appear to end in the splanchnic center in the rostral part of the cord, since the longitudinal tract disappears in all cases (except *Petromyzon*?) caudal to the first few segments of the cord. Near the junction with the medulla these bundles approach the dorsal raphe and rise to the dorsal surface. Here a larger number of fibers from the same sources decussate (*commissura infima* HALLERI) and end in a median nucleus first described by CAJAL (1) for mammals. This commissure and nucleus mark roughly the limit between the cord and medulla. The splanchnic center continues rostrad from the commissure, in lower forms continuous with the median nucleus, and becomes greatly enlarged as the lobus vagi of fishes or the nuclei of the fasciculus communis or solitarius of higher forms. Its position in the medulla is the same as in the cord, ventro-median to the somatic sensory center. It continues forward to the point of exit of the fasciculus communis VII root and there abruptly terminates.

Although considerably larger in the brain than in the cord of all vertebrates, the splanchnic center varies enormously in size in the lower vertebrates. This variation is due in part to differences in the extent of visceral area to be innervated, but far more to the differences in the number of end-buds, especially in the skin. In *Petromyzon*, where end-buds are few, the splanchnic center in the medulla is very small in its rostral part, is largest near the commissure, and is larger in the cord than in other vertebrates. The center is simpler in structure than in higher fishes. In selachians (10) it is smaller than in teleosts, in ganoids it is well developed, while in some teleosts in which end-buds are exceedingly numerous, it forms the largest and most conspicuous division of the medulla. It is noteworthy that the splanchnic sensory center does not extend as far rostrad as the splanchnic motor, and that both are far out-reached by the somatic divisions.

The most conservative elements in the cord and brain are purely central and do not belong to either of the main divisions of the central system. These are the connective elements, the cells which set up connections between successive or distant segments of the brain and cord. These tract and commissural cells are present in almost all parts of the cord and in the medulla they and their tracts continue to form the bulk of the ventro-lateral region. They are practically absent from both of the sensory centers, but are intermingled with the motor cells.

The decussation of fibers ventral to the ventricle is continued from the cord into the medulla and is greatly increased by the large number of internal arcuate fibers, secondary fibers from the somatic sensory centers to the tectum opticum. The dorsal commissure of the cord is interrupted in the medulla by the choroid plexus and its elements are gathered in two commissures, the commissura infima HALLERI and the cerebellar commissure. The former is at the caudal end of the medulla and represents the splanchnic portion of the dorsal commissure of the cord. The latter connects the somatic centers, although it is not clear that it contains the same somatic elements as does the dorsal commissure.

From this survey it appears that the hind brain, including the cerebellum, is readily reducible to four longitudinal zones or columns which correspond directly to the chief zones of the cord, and that where modifications of these columns are found in the hind brain they are due to modifications of the corresponding peripheral end-organs in the head region. An exception to this statement must be made for the lower olive, a body which appears in the lowest craniates (*Petromyzon*, *Acipenser*) as a collection of cells about the ventral roots of the occipito-spinal nerves (*hypoglossus*), whose neurites break up among the ventro-lateral tracts of the opposite side. The only suggestion which the writer is able to offer toward the interpretation of the olive is that its cells must be derived from the commissural cells of the region, and that the formation of a special nucleus may be in some way connected with the degeneration and disappearance of dorsal roots in the occipital region. The

disappearance of dorsal roots would leave commissural and tract cells without function. It seems possible that some of these have acquired secondary functions which have prevented their disappearance.

The disposition of the secondary central tracts constitutes a distinction between the somatic and splanchnic sensory divisions which the writer has pointed out (12) and wishes to emphasize here. The somatic sensory nuclei send internal arcuate fibers to the tectum; the splanchnic centers send their fibers as an uncrossed secondary vagus tract to a nucleus at the anterior end of the medulla. The connections of the splanchnic central apparatus are imperfectly known, but it is clear that they are radically different from those of the somatic centers. It is an important part of the conception set forth in this paper that the somatic and splanchnic sensory divisions are distinct in their central relations. It is obvious that if both sent their secondary tracts to a common center they could not perform separate functions. The central reflex apparatus is not less significant and important than the peripheral distribution of the nerve components.

The attempt to reduce the mid, 'tween, and fore brain to terms of these four functional divisions leads us into a field where few data for certain conclusions are at present to be found. In the base of the mid brain, however, as noted above, the somatic motor center is well developed and it extends forward in the thalamus nearly to the rostral end of the brain axis. Similarly the tract and commissural cells are present in the base and lateral walls of the mid brain. Neither the sensory nor the motor splanchnic column is represented rostral to the medulla. If any further comparison is to be found between the mid brain and the chief divisions of the cord and medulla, it must exist between the tectum and the somatic sensory centers. Since the retina is a part of the brain wall, the optic nerve is to be regarded as a central tract and the tectum, so far as it is related to the retina, as a coordinating or distributing center between other brain centers. But the paired eyes are phylogenetically younger than the brain centers with which they are connected,

and an attempt to compare the chief and most fundamental divisions of the mid brain with those of the cord must make use, if possible, of the oldest part of the mid brain. A comparison of the tectum of *Petromyzon* with that of higher fishes and amphibia shows that the secondary center for the somatic sensory column is nearly as well developed in *Petromyzon* as in the higher forms, while the elements belonging to the optic apparatus are few and poorly differentiated, corresponding to the slight development of the eyes. It therefore seems to be a warranted assumption that the nucleus of the internal arcuate fibers in the tectum represents the most fundamental structure in the dorsal part of the mid brain. The nervous elements of this nucleus more nearly resemble the elements of the somatic sensory centers in their size, form, stage of development, and their arrangement, than those of either of the other columns. The suggestion may be ventured that the secondary center in the tectum was originally a more rostral portion of the somatic sensory column, that the internal arcuate fibers are to be interpreted as crossed connectives between distant segments of the somatic sensory column, which are probably represented at other levels by the external arcuate fibers. This implies the following conception of the arrangement of the somatic centers in primitive vertebrates: certain fibers served as crossed connectives from lower to higher segments of the somatic sensory column, while others probably made indirect connections with the motor centers by way of the commissural and tract cells. There has been a gradual tendency for the connectives to pass forward to the most rostral part of the somatic sensory column and as a result this region has become differentiated as a special secondary nucleus, which receives no sensory root fibers, but only these connectives. At the same time it has come about that the fibers which make connections between the sensory and motor centers arise only from this special region. The result is to give a more complex and efficient distributing and coördinating mechanism; a more highly organized apparatus for somatic reflexes, which is more capable of producing definite movements adapted to specific ends. This

hypothesis receives some further support from the fact that the fibers from the tectum, at least for the most part, connect not with the motor centers directly but with intermediate neurones.

The fact last mentioned, taken together with the connections of the lobi inferiores, suggests an interpretation of the latter. These lobes are the hypertrophied ventral region of the 'tween brain whose tracts go, partly direct, partly crossed, to the medulla and the fore brain. The lobes receive important tracts from the tectum and from the secondary olfactory centers. Thus the inferior lobes do not stand in immediate connection with any sensory center, but do send fibers to make (probably) immediate connections with motor centers. With respect to the tectal tracts these neurones stand in the same relation as intermediaries between the tectum and the motor centers, as do the commissural and tract cells in the medulla which receive the endings of the tractus tecto-bulbaris. This description places the cells of the inferior lobes in the category of commissural and tract cells. The inferior lobes may be regarded as a special collection, at the rostral end of the brain axis, of these cells which in general form the commissural and connective elements in the central nervous system. The fibers going from the inferior lobes to the fore brain arise chiefly from the corpus mamillare. The tracts are essentially dorso-ventral and not longitudinal. They are to be regarded as a late formation due to the influence of the olfactory and optic apparatus. Fibers from other cells of the same nucleus pass backward to the medulla.

The presence of the somatic motor column in the thalamus and the fact that this column extends practically the whole length of the central nervous system, have been noted. Surrounding the nucleus of the somatic motor fasciculus laterally and dorsally the central grey of the 'tween and mid brain is composed of rich masses of cells which in the lower craniates constitute for the most part a nucleus diffusus, but which form the material for later differentiated special nuclei. One of these is the nucleus of the posterior commissure, already distinguishable in *Petromyzon*. This does not at present offer any data

for comparison with structures in the cord or hind brain. Other nuclei are said to receive the descending tracts from the corpus striatum. These may probably be referred to the category of commissural and tract cells.

There remains to be considered the dorsal part of the brain at its extreme rostral end. This region includes the dorsal half of the primary fore brain. In its caudal part ('tween brain) diverticula of the dorsal brain wall form one or more primitive eyes, possibly paired. These are in all probability the most primitive sense organs of the head region which still persist in craniates. Since they are diverticula of the brain wall, neither they nor their brain centers can be compared in any way with either of the four chief divisions of the hind brain and cord. The centers are either too far degenerated to be studied or are dominated by other organs into whose service they have come.

The chief part of the region under consideration is made up of the olfactory apparatus. This is doubtless much younger phylogenetically than the pineal structures, but also much more important. The olfactory nerve has been compared in various ways with the typical cranial and spinal nerves. The tendency in late years has been to abandon this comparison, and an examination of the peripheral and central features of the olfactory apparatus will show that the attempt to bring it into the same category with the typical cranial nerves is wholly fruitless. The cells from which the fibers of the olfactory nerve arise are situated in the epidermis, while the ganglion cells of the typical nerves have been derived from the cord or brain. Evidence of this is found in *Amphioxus*, where the sensory fibers are sent out from cells lying in the cord, and in the giant ganglion cells of the cord of fishes, which have the same relation (5, 6, 11). These facts show that the olfactory nerve is the only one in which fibers run from peripheral sense cells into the central system. In all other cases, cells in the central system (or derived from it) send fibers out to end in relation with sense cells in the epidermis. The olfactory fibers on entering the brain break up immediately in the glomeruli, in contrast to the conduct of the typical sensory root fibers which run a longer or shorter dis-

tance in the cord or brain to end in other segments. Further, an examination of the central arrangement of the olfactory apparatus shows that the chief characteristics of central sensory nuclei and tracts are wanting and that the olfactory apparatus presents a quite peculiar arrangement.

The end-nucleus of the olfactory nerve is the olfactory lobe, situated in the morphologically dorsal part of the fore brain near its extreme rostral end. In this there are found cells of the I and II types which in the lower vertebrates have not reached any considerable degree of specialization. Their neurites are sent to several nuclei which are also found in the morphologically dorsal part of the fore brain (epistriatum, area olfactoria, and nucleus thæniæ). The fibers are partly direct, partly crossed, the decussation taking place in the anterior commissure, or in a separate moitie of the same, the olfactory com-

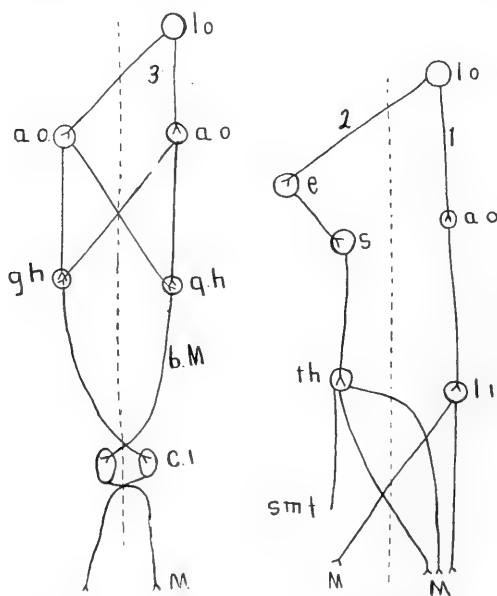


Fig. 2.—Diagram of the central olfactory apparatus. *a. o.*—area olfactoria; *b. M.*—bundle of MEYNERT; *c. i.*—corpus interpedunculare and other nuclei of the bundles of MEYNERT; *e.*—epistriatum; *g. h.*—ganglion habenulæ; *l. i.*—lobus inferior; *l. o.*—lobus olfactorius; *M.*—motor centers; *s.*—striatum; *s. m. f.*—somatic motor fasciculus; *th.*—thalamus.

missure. The secondary nuclei now send the stimuli to the motor centers over three quite distinct paths. These paths are shown in the accompanying figure. The first path consists of direct tracts to the ventral side of the rostral end of the brain, the lobi inferiores, from which the impulses go over direct and crossed tracts to the bulbar motor centers. The second and shortest path is by way of the epistriatum and striatum to the nucleus of the somatic motor fasciculus. It is possible that this path has another branch in the thalamus by way of the central grey belonging either to the category of commissural and tract cells or to the nucleus of the posterior commissure. The third path is by way of the ganglia habenulæ and the bundles of MEYNERT. The first step of this path is the tractus olfacto-habenularis which connects dorsal grey masses of the fore brain with dorsally situated grey masses of the 'tween brain. However, the ganglia habenulæ are separated by the choroid plexus and it may be that they are not morphologically dorsal, but lateral. The tracts decussate in part or wholly at the dorsal surface of the 'tween brain before ending (commissura superior). The second step in this path connects the ganglia habenulæ (after decussating) with a special nucleus in the base of the mid brain which shows a close resemblance to a collection of commissural cells. The cells of this nucleus, finally, send their neurites to the motor centers of the opposite side of the medulla.

The olfactory apparatus thus consists of a primary sensory center, the lobe; of secondary dorsal centers in the fore brain; and of tertiary centers in the 'tween brain, one ventral, one in the central grey, and one lateral or dorsal. The nucleus of the second path in the central grey is at least in part motor, the ventral nucleus has been interpreted above as a special collection of commissural and tract cells, while the dorsal path requires the bundles of MEYNERT to connect the 'tween brain center with a nucleus of the grade of commissural cells. Thus the central path is shortest, the ventral next, and the dorsal longest, but the ventral is probably the oldest or most primitive and the most general in its scope. The path by way of the

striatum is crossed and probably serves to make some special connections. The dorsal path is distinguished by repeated decussations in its course. The result of the complicated arrangement is to ensure stimuli from either olfactory lobe reaching the motor nuclei of both sides, which is not surely accomplished by either the first or second paths. Even in the most primitive craniates no part of this apparatus shows any essential likeness to the structure of either the somatic or splanchnic sensory division of the nervous system.

This examination also shows that the olfactory has no claim to be considered a segmental nerve. It is rather to be considered as a special nerve and its sense organ as the only really special sense organ of peripheral origin (the eye being of central origin and the ear belonging to the category of lateral line organs). The olfactory organ and central apparatus lie, indeed, in the first three head segments, but they do not serve in any way to define those segments, since they have no points of comparison with structures of typical segments. Toward the definition of the more anterior head segments the discovery of certain rudimentary structures has recently furnished promising material. Of these, it is possible that the "accessory olfactory nerves" described by PINKUS (16) and LOCY (14) belong to two of the segments which enter into the primary fore brain, while the *N. thalamicus* of PLATT (17) belongs to the mid brain. The latter nerve is probably a remnant of a general cutaneous nerve which formerly had its central ending in what is now the tectum opticum. The centers of the "accessory olfactory nerves," however, have become so highly modified in the service of the olfactory organ that they can no longer be intelligently compared with the sensory centers of more caudal segments. It is probable that they originally formed the most anterior portion of the somatic sensory column.

It is noteworthy that of the commissures in the mid, 'tween, and fore brain, the ventral ones (*commissura ansulata* and *decussatio postoptica*) are directly comparable with the ventral commissures of the spinal cord and medulla. Of the dorsal commissures, on the other hand, only the dorsal decus-

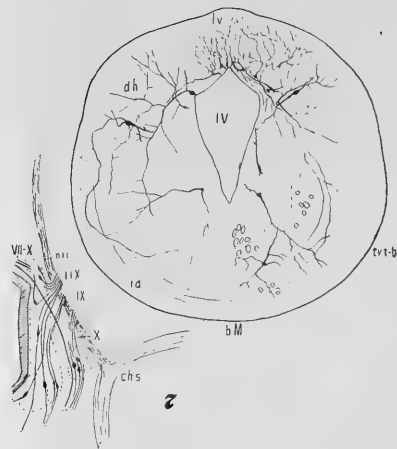
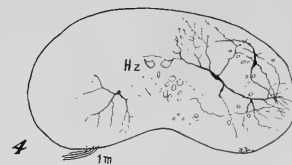
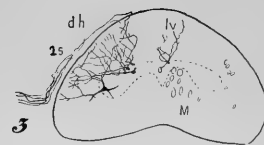
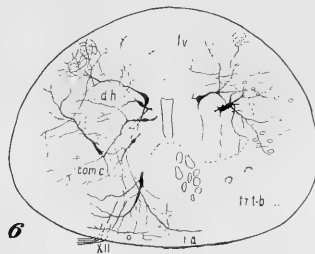
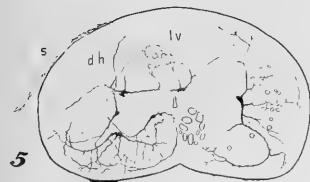
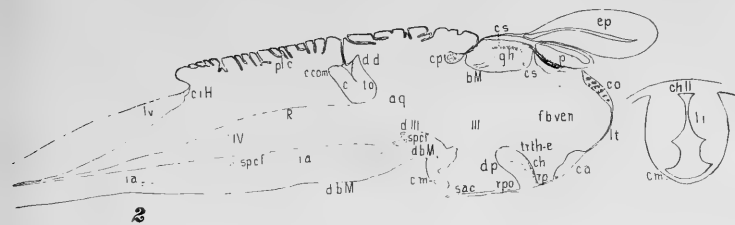
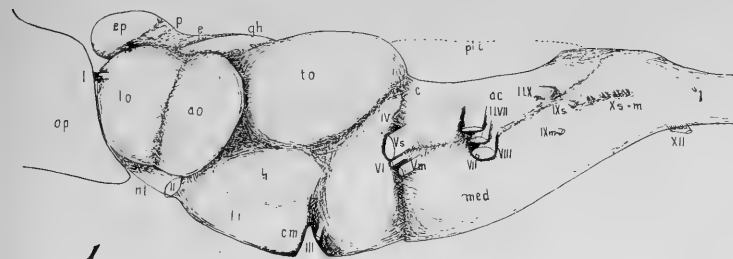
sation of the tectum can be compared with the (somatic sensory portion of the) dorsal decussation of the cord. The posterior, superior, and anterior commissures are all peculiar to themselves, not comparable with any structures in the hind brain or cord.

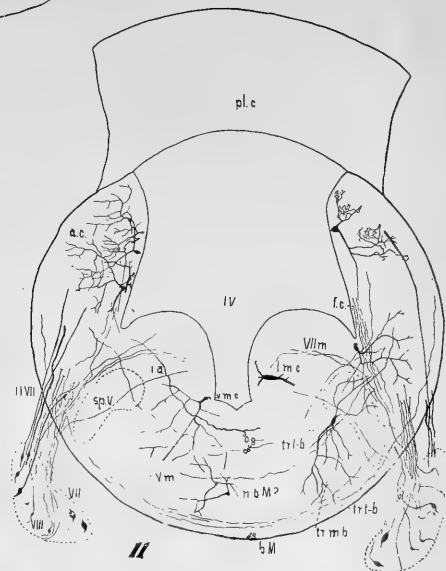
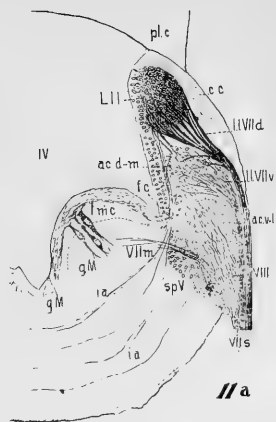
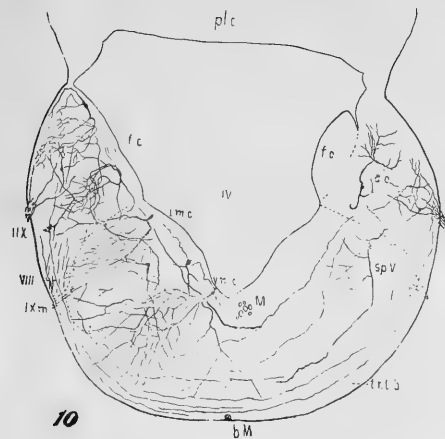
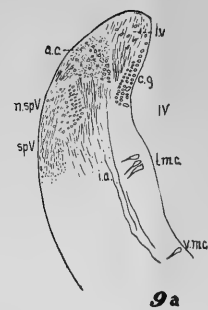
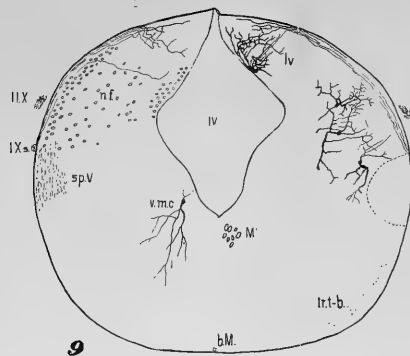
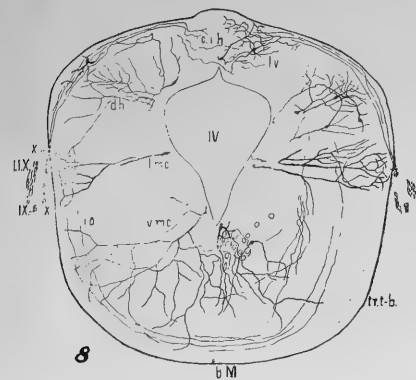
The general result of this study is to divide the nervous system into four main functional divisions: somatic and splanchnic sensory and motor divisions. The recognition of these divisions together with the connective elements in the central nervous system gives an adequate basis for the description of the spinal cord and the hind brain. The somatic motor division extends forward almost to the extreme rostral end of the brain axis, and there is reason for thinking that a large part of the mid, 'tween, and fore brains consists of cells belonging to the same category as the connective elements. The splanchnic sensory and motor divisions do not extend rostrally beyond the medulla. The somatic sensory division, on the other hand, includes the cerebellum and probably also the tectum opticum. There are certain parts of the central grey matter in the rostral region of the brain (for example, the nucleus of the posterior commissure and the corpus striatum) which hold such relations as to defy attempts to interpret them as modified representatives of any structure in the spinal cord or hind brain. The same is to be said of the dorsal part of the brain at its extreme rostral end. A part of this region seems once to have received somatic sensory nerves, but it has now so far lost its primitive character that attempts at comparison with more caudal regions fail. This is due in part to the great development of the olfactory apparatus, but it is probable that a portion of this region is to be regarded as a cephalic enlargement of the central axis older than the typical structure of the vertebrate nervous system. Behind this region the nervous system consists of four longitudinal divisions, each of which has its peculiar function and presents a segmental arrangement corresponding to the metamerism of the other system of organs.

*Morgantown, W. Va.,
November 17, 1901.*

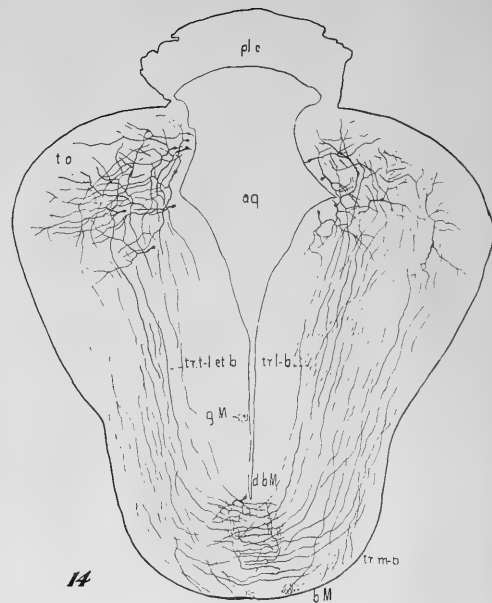
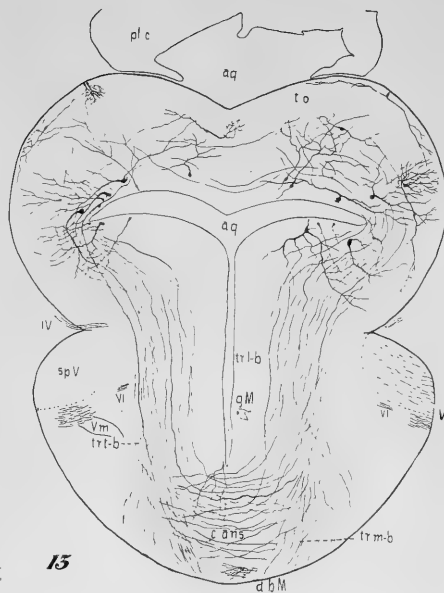
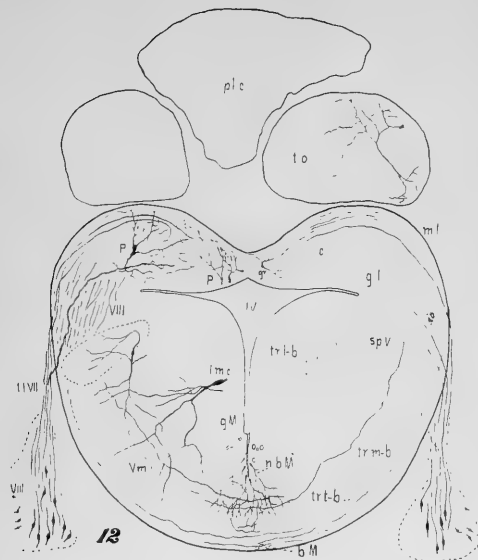
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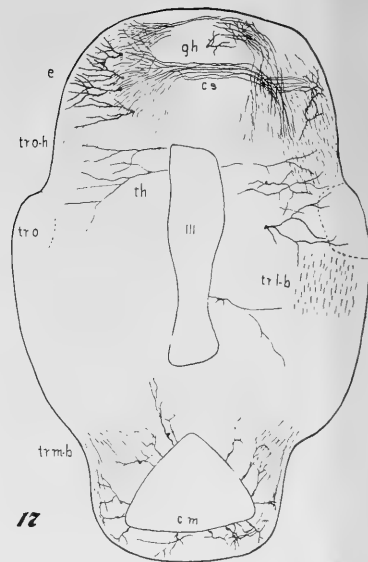
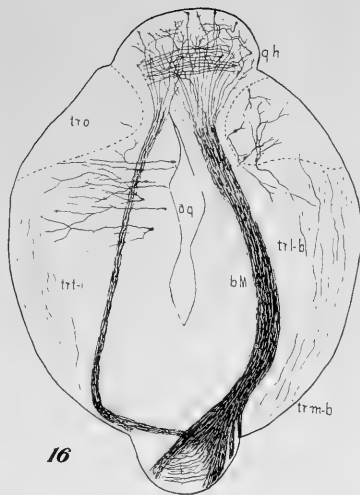
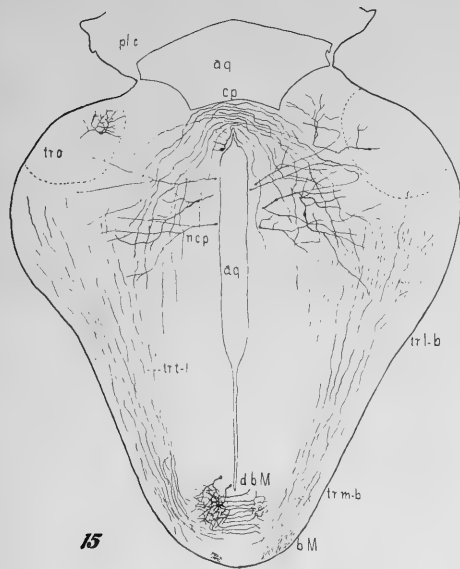




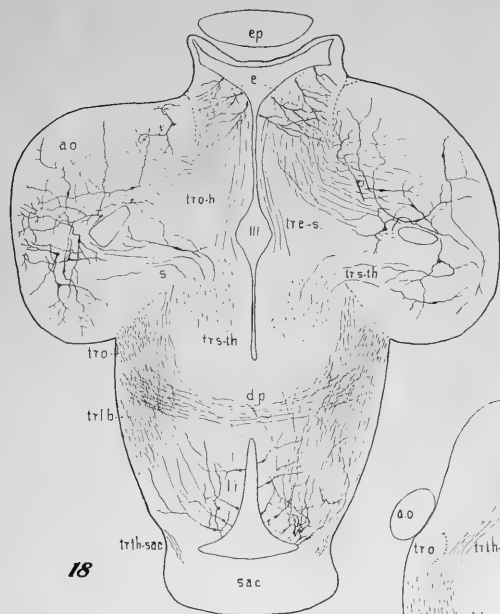




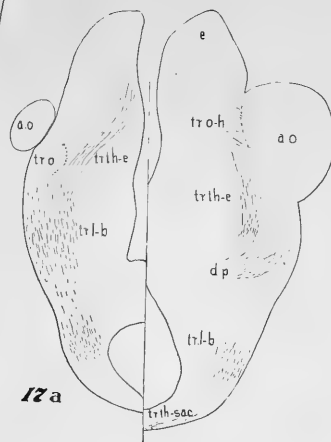




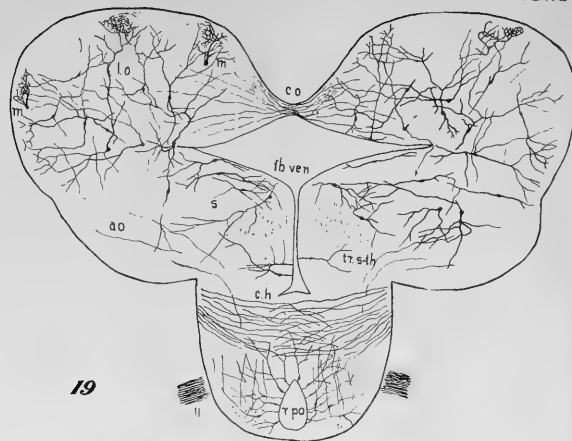




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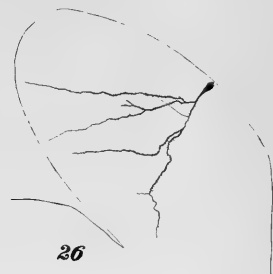
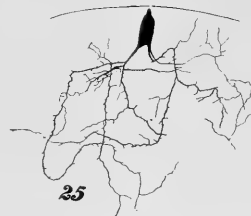
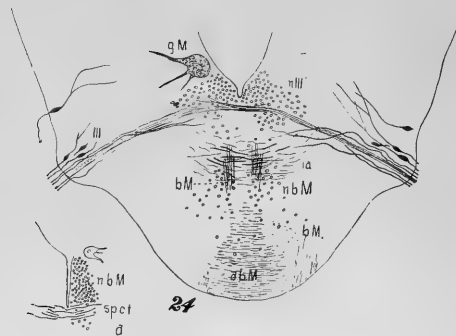
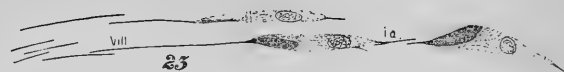
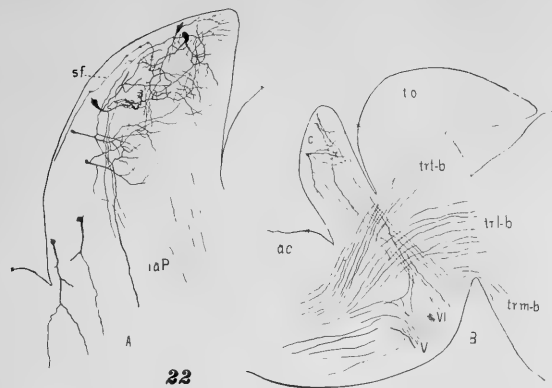
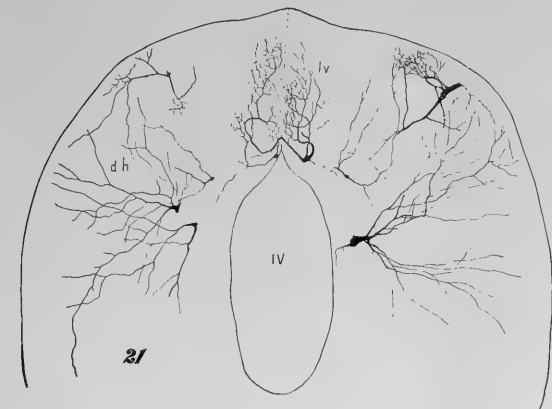


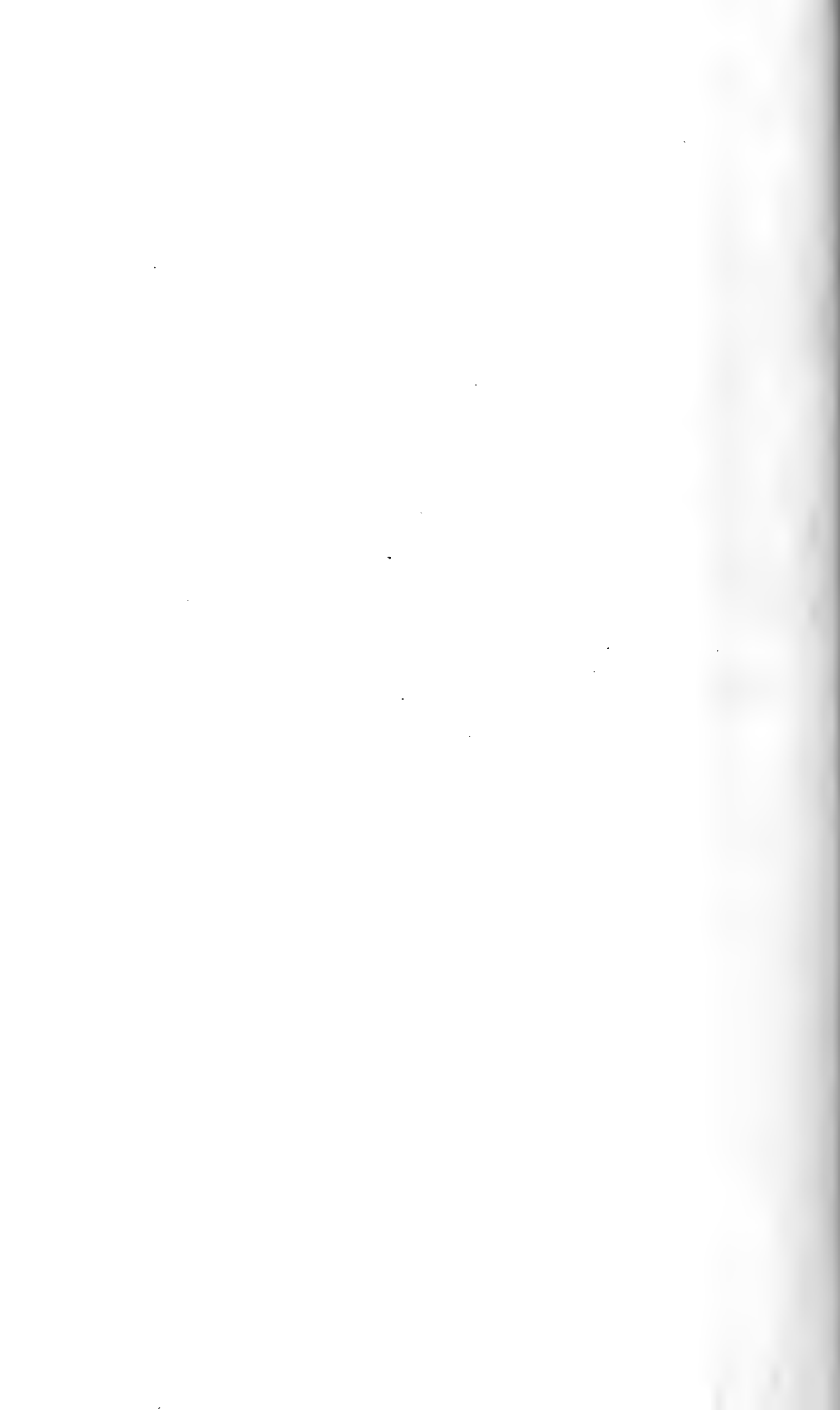
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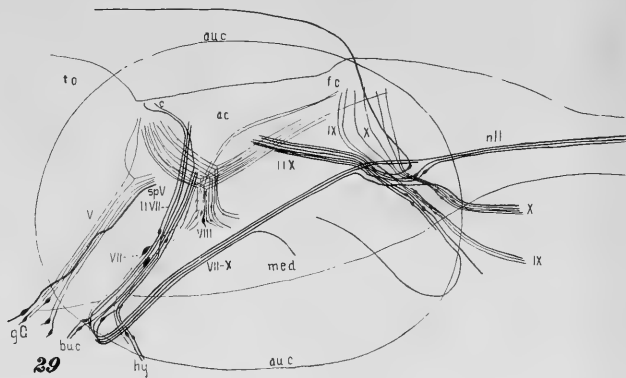
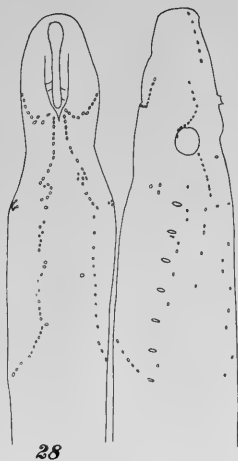
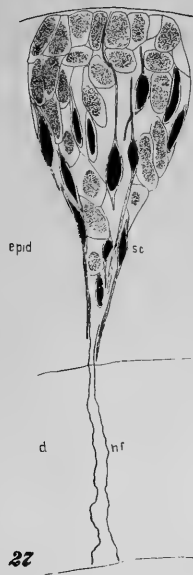


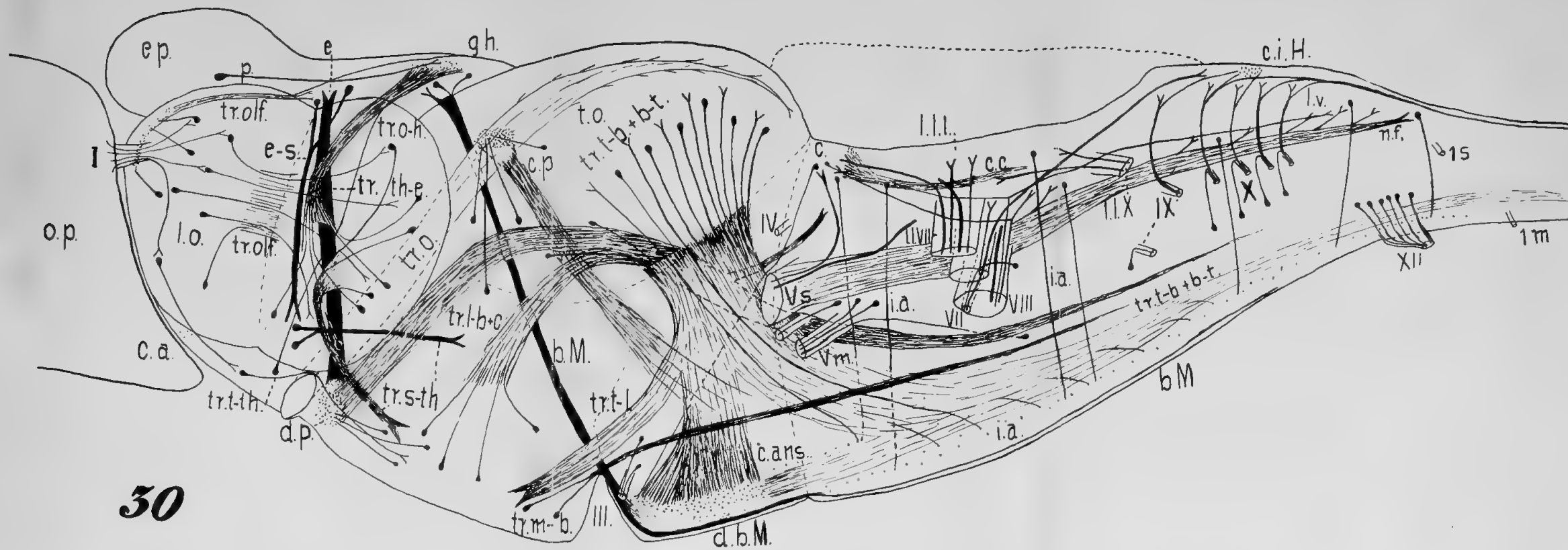
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JOURNAL OF COMPARATIVE NEUROLOGY.

NUMBER AND SIZE OF THE SPINAL GANGLION
CELLS AND DORSAL ROOT FIBERS IN THE
WHITE RAT AT DIFFERENT AGES.

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I. INTRODUCTION.

The present investigation was undertaken for the following reasons:

(1). In my previous paper (1901, I) on the small spinal ganglion cells in the white rat, these cells were considered to be immature and growing. In that paper, the following statement was made, "From these several observations the writer concludes that the small cells of the spinal ganglion are in a growing state or in a more or less permanently immature condition. The growing fibers (1899) which are found in an adult frog might, therefore, very well be formed by the axones of these latent cell-bodies." If this interpretation was correct, then the number of the small cells should decrease with age, and at the same time, the number of the large cells should increase.

(2). In a second paper (1901, II), the writer made the following suggestion concerning the possibility of the division of the nerve cells in an adult animal, "We can only say, at present, concerning the division problem that the nerve cells in vertebrates, as well as invertebrates, have the centrosome and the sphere, which are regarded as the dynamic centers of the mitotic divisions, and, further, that this centrosome is able to take the first steps of division under certain forms of stimulation, as has been observed by some investigators; but in the normal state the centrosome in an adult cell presents slight morphological differences from that of the embryonic cell, which we interpret as the beginning of degeneration." The writer said further, "In order to give a positive answer to the question (division-problem) above mentioned, it seems to me that the only safe and reliable method consists in counting the nerve cells in the spinal ganglia of a given species of animal at different ages, and thus determining whether there is any increase in their number."

The present investigation consists of a series of enumerations of the spinal ganglion cells and dorsal root fibers, undertaken with a view to settling these questions.

II. MATERIAL AND TECHNIQUE EMPLOYED FOR THE PRESENT INVESTIGATION.

Male rats having a body weight of 10.3, 24.5, 68.5 and 167 grams respectively, were employed. The exact ages of these rats are not known but approximately their weights in grams represents their ages, in days. The ganglia examined were the VI cervical, IV thoracic, and II lumbar. As soon as the dorsal roots with the corresponding ganglia were removed from the cord they were placed on card-board without disturbing the natural length of the nerve roots and preserved in 1% osmic acid solution for 24 hours. After this the specimens were detached from the card-board and washed in running water for 6 hours. Afterward, the specimens were carried through the graded alcohols and embedded in paraffin according to the usual procedure.

For the counting and measurements of the cell-bodies, the sections were cut 12 micra in thickness, while for the nerve fibers 6 micra was found to be a convenient thickness. For the enumeration of the nerve-fibers, the writer employed exclusively the photographic method as used by Dr. HARDESTY (1899) in this laboratory; since, by this method, the enumeration of the nerve fibers is made most accurately and with least fatigue. The countings of the nerve-cells, however, was done with the net under the microscope, using oc. $4\times$ obj. 8 mm. of ZEISS. Since the large nerve cells (50 micra in diameter), as well as the nuclei (16 micra in diameter) may appear in more than one section, the count was made by enumerating the nucleoli. Fortunately, the presence of multi-nucleoli is very rare in the large cells, though it is not uncommon in the small or smallest cells. Under these conditions, an error in the counting would occur only when one nucleolus was in one section and the other in a second, an arrangement so rare that it may be neglected.

In studying the numerical relations between the cells in the spinal ganglion of several sacral nerves of the rabbit, and the fibers in the corresponding dorsal nerve roots, LEWIN (1896) first counted the cells by enumerating the nucleoli as they appeared in successive sections. This gave him such a large number of cells that he feared that an error had been introduced, owing to the presence of double nucleoli. To correct this, he made another enumeration of cells by the following method. He counted the number of cells which appeared in all of the sections, each section being 10 micra in thickness, and then estimated the average diameter of nerve cells by taking the mean of largest and smallest there present. Employing this average diameter, he then calculated the number of cells. This gave a smaller number than that obtained by counting the nucleoli. The error introduced, however, by employing the average diameter, owing to the variable ratios of large and small cells in any given ganglion, is much greater than that connected with the first and simpler method. For this reason the direct enumeration of the nucleoli, due care being taken to avoid counting double nucleoli, has been used in this case.

In most cases we can determine without any trouble whether in successive sections we are dealing with two parts of the same cells or different cells, and thus the actual error introduced in this way is probably very small. The determination of the small and large cells was made according to the method used in my previous paper on the spinal ganglion cells (1901, I). The class of intermediate cells recognized in that paper was neglected in this study, these cells being classified as large or small according to their diameters. At first, the entire number of the cell-bodies including both large and small, was enumerated. Then the large cells alone were enumerated and their number was deducted from the total, thus giving the number of small cells.

III. ON THE SPINAL GANGLION CELLS.

A. Total Number of the Spinal Ganglion Cells at Different Ages.

The number of the nerve cells in the spinal ganglia has been determined by several investigators:

FREUD ('78), in the spinal ganglia of *Petromyzon*; HODGE ('88) in the spinal ganglia of the frog; GAULE and LEWIN ('96) in the spinal ganglion of the rabbit; and BÜHLER ('98) in the spinal ganglion of the frog. So far as I am aware, no investigators have ever enumerated the number of the spinal ganglion cells at different ages in the same animal.

The following table shows the total number of the spinal ganglion cells in the three ganglia at different ages:

TABLE I.

Total Number of Cells in the Spinal Ganglia of Male White Rats at Different Ages.

Body Weight Grams.	VI Cervical.	IV Thoracic.	II Lumbar.
10.3	10996	7142	8315
24.5	9793	7068	8200
68.5	11772	7611 ¹	9514 ¹
167.	12200	7406	9442
Average number	11140	7306	8867

¹ These figures were obtained from a rat having a body-weight of 69 grams and not from the one weighing 68.5 grams, the cervical ganglion of which was alone counted.

As the above table shows, the cervical spinal ganglion contains the greatest number of the cells; the lumbar comes next, while the thoracic contains the smallest number. The most interesting as well as most important point shown by Table I is the approximate constancy of the total number of the ganglion cells during the period chosen. The excess of the number of the cells in the rat of 167 grams over that of 10.3 grams is 10% in cervical and 13% in lumbar, while in the thoracic it is 3.5%. The question at once arises whether this excess means the increase of the number of the cell-bodies with age or whether it is due to individual variation merely. The only argument in favor of interpreting these figures as showing an increase of the number of cells with age is the fact that in the 68.5 and 167 gram rats, the number of cells is greater than in the 10.3 and 24.5 gram rats. Against the idea of the increase is the fact that the 24.5 gram rat shows fewer cells than the 10.3 gram rat, and that in the thoracic and lumbar ganglia the 167 gram rat shows fewer cells than the 69 gram rat. Moreover, there is no indication of cell division in these ganglia. We therefore consider the differences here observed as due to individual variations. The total number of cells is however the sum of two sorts: the small and the large.

BÜHLER ('98) made the following suggestions concerning the small cells: "Es kommt, wie ich mich bei Frosch und Kröte und auch beim Kaninchen überzeugen konnte, physiologischer Weise zum Untergang speciell der grossen Spinalganglienzellen. Die Degeneration verläuft in verschiedenen Formen und allem Anschein nach wenig rapid. Man sieht in einem Spinalganglien des Frosches ca. 20-25 untergehende Zellen, beim Kaninchen relativ noch viel weniger. Die verloren gegangenen Zellen müssen ersetzt Werden, und dies geschieht Wahrscheinlich dadurch, das eine der kleinen durch Wachstum ihre Stelle einnimmt. Da nach dem frühesten Jungenstadium eine Vermehrung von Nervenzellen nicht mehr Vorkommt, muss das Spinalganglien, um für die Zeit des Lebens functionsfähig bleiben zu können, in der Anlage genügendes Ersatzmaterial in Gestalt von Reservezellen mitbekommen. Genauere

Untersuchungen hierüber zu machen, bin ich indess noch nicht in der Lage gewesen."

The above interpretation given by BÜHLER concerning the small cells can not be accepted as far as white rats are concerned, for he regarded the small cells as replacing the degenerated large nerve cells; if this were the case, then the total number of the spinal ganglion cells must decrease, but the preceding table shows that the total number is approximately constant.

B. Ratios of Large to Small Cells.

Our assumption that the small cells are in an immature or growing condition, and are more or less transformed into large cells, is proved from the following table which shows that the relative number of the large cells steadily increases.

TABLE II.

Showing the ratios of the large to the small cells.

	Body weight Grams.	Large Cells.	Small Cells.	Total Number.	Ratio L. and S.
IV Cervical	10.3	2526	8470	10996	1:3.4
	24.5	2395	7398	9793	1:3.0
	68.5	3546	8226	11772	1:2.3
	167.0	5080	7120	12200	1:1.4
IV Thoracic	10.3	1557	5585	7142	1:3.5
	24.5	1824	5244	7068	1:2.9
	69.0	2370	5241	7611	1:2.2
	167.0	2902	4404	7406	1:1.5
II Lumbar	10.3	1902	6413	8315	1:3.4
	24.5	2044	656	8200	1:3.0
	69.0	2934	6580	9514	1:2.2
	167.0	3677	5765	9442	1:1.5

From the table it is clear that the number of the large cells at 167 grams in each region is nearly twice that at 10 grams, showing a ratio of 1:2 approximately. Further, the ratios between the large and small cells in different regions of the animal at the same age is always constant. For instance, the 10.3 gram white rat shows a ratio between the large and small at the three regions of 1:3.4, 1:3.5 and 1:3.4 respectively; in the 24.5 gram rat the ratio is 1:3, 1:2.9 and 1:3 respectively, etc. Finally, the 167 gram rat gives the ratio of 1:1.4 to 1:1.5. From this we can say that each spinal ganglion in the individual at a

given age contains the same proportional number of the small and large cells. The percentage of the small cells in different regions at the same age holds nearly the same proportion. An adult white rat (167 grams) contains, therefore, in each spinal ganglion still 60% of the small cells which were left in an undeveloped condition.

Since the small cells are increasing in diameter from 10.3 grams to 167 grams, the same standard in size cannot be employed in each case. The following table shows the maximum diameters of the small cells at different ages. The small cells, however, cannot be determined by measurement only, for in some cases the cells show evidently the characteristic structures of the large cells in spite of the diameter corresponding to the following table. For this reason, the proper determination of the number of the small cells will not be obtained by measurement only. In this case, therefore, the small cells are those having the diameter less than the diameter of the cell recorded in the table, and at the same time showing the structure characteristic of the small cells as previously determined. (1901, I).

TABLE III.

Showing the Maximum Diameters of the Small Cells at Different Ages.

Regions.	Body-Weights.			
	10.3	24.5	68.5	167
VI Cervical	22.4	24	25.6	28
IV Thoracic	18.8	21	22.8	24
II Lumbar	21.4	22.4	24	27

The diameters of the small cells here given are slightly larger than those given in the table of the previous papers (1) on the spinal ganglion cells in the white rat. This difference is mainly due to the method of selection of the cells for the measurement. In this case two largest small cells from each section (68.3 and 167 grams), and three largest small cells from each section (10.3 and 24.5 grams) were selected for measurement; while in the previous case five largest small cells from each section were measured. Thus, in the latter instance, reducing the average.

IV. THE DORSAL ROOTS.

A. Total Number of the Dorsal Root Fibers at Different Ages.

The number of the fibers of the dorsal roots has been enumerated by several investigators. HOLL ('75) counted the fibers in the two roots and the trunk of three of the lumbar nerves of the frog in order to compare the total number of the fibers in the two roots with that of the corresponding trunks; FREUD ('78) in studying the relation of the dorsal root fibers to the spinal ganglion cells made counts on *Petromyzon*; STIENON ('80) in studying the relation of the dorsal root fibers to the cells of the spinal ganglion made two counts of the fibers in the two roots and in the trunk; HODGE ('88) counted in the frog the number of fibers of the dorsal roots and the number of the cells in the spinal ganglia of several nerves in order to show the numerical relation between the two; BIRGE ('82) made counts on the dorsal and ventral roots and at the same time the trunk of the several spinal nerves of the frog in order to compare the numbers in these three different regions, as well as to show the relative increase of the fibers and the cells in the anterior horn according to different weights of the frog; GAULE and LEWIN ('96) counted the fibers contained in the two roots and in the trunk and dorsal branches of three of the sacral nerves as well as on the cells of the corresponding spinal ganglia of the rabbit, in order to determine the number in each case; BÜHLER ('98) undertook the problem in order to compare the number of fibers with the number of cells in the spinal ganglion in the frog; HARDESTY ('99) counted in eight spinal nerves, the two roots and trunks, in order to determine the number in each case, and he further extended his studies ('00) on the frog in order to compare the number of fibers in the same regions at different seasons, but in this latter case, the VIth. spinal nerve was used exclusively; DALE ('00) has made similar counts of the fibers in some of the coccygeal, two thoracic and one lumbar nerve of the cat. All investigators (HODGE, GAULE and LEWIN, and BÜHLER) who have compared the number of cells in

the spinal ganglion with the number of fibers in the dorsal nerve root, have found a more or less striking excess of cells in the ganglion.

So far as I am aware, no investigators have ever enumerated the number of the spinal nerve fibers in any mammalian from the period just after birth to maturity. The following table shows the total number of the dorsal root fibers in the roots belonging to the selected ganglia.

TABLE IV.

Showing the Total Number of the Dorsal Root-Fibers at Different Ages in the White Rat.

Body-Weight Grams.	VI Cervical.	IV Thoracic.	II Lumbar.
10.3	1998	607	723
24.5	2569	863	911
68.5	3683	1420 ¹	1317 ¹
167.0	4227	1522	1644

From the Table IV it is clear that at any given age the total number of the fibers differs in the three roots of the same animal. It is also shown that the number of the fibers is greatest in the cervical region and that the numbers in the lumbar and thoracic regions follow in order named, except in the case of the 68.5 gram rat, where the number of the fibers is greater in the thoracic than in the lumbar nerve. Taking the number of the fibers in the thoracic as a standard (167 grams), the following ratios are obtained: Thoracic 1, lumbar 1.07, cervical 2.9. Briefly stated, the total number of the dorsal root fibers in the VI cervical nerve at 167 grams is approximately three times as great as in the case of either the thoracic or lumbar at the same age.

The observations of BIRGE ('88) and HARDESTY ('99) on the frog show an excess of the dorsal root fibers in both cervical and lumbar enlargements, and estimates made by STILLING of the area of the cross-section of the dorsal roots in man, show the same thing.

¹ These figures were obtained from a rat having a body-weight of 69 grams and not from the one weighing 68.5 grams, the cervical ganglion of which was alone counted.

The following table will show the relative increase of the dorsal root fibers in the three roots at different ages.

TABLE V.

Showing the Relative Increase of the Fibers at Different Ages.

Body Weight Grams.	VI Cervical.	IV Thoracic.	II Lumbar.
10.3	1.	1.	1.
24.5	1.28	1.42	1.26
68.5	1.84	2.33	1.82
167.	2.11	2.5	2.27

As will be seen from the Table V, the relative increase of the fibers in each region is quite gradual. From the same table it is clear that the fibers in the cervical increase in nearly the same ratio as those of the lumbar nerve, while the fibers of the thoracic, increase more rapidly than the others. This rapid increase of the number in the thoracic nerve will be discussed later on.

B. Ratios Between the Completely Formed and Immature Fibers.

The cross section of the dorsal root at birth, stained with osmic acid presents two kinds of the fibers: one shows clear outline and stains an intense black, while the other shows clear outline and stains with the osmic less intensely, or remains nearly unstained. A careful observation with high magnification, however, reveals to us that the former is surrounded by a sheath which contains an abundance of myelin substance, while the latter possesses a sheath with less myelin substance, which substance sometimes appears as black dots at the side of the sheath. From these facts (WLAŚSAK '98) the present writer identified the former as the completely formed fibers while the latter he considered as immature. The diameters, however, do not serve to distinguish an immature from the completely formed fibers, for the diameter of the former exceeds, in some cases, that of the latter. Therefore, these distinctions can be determined only by examining the fiber with high magnification, and thus determining whether the sheath contains the full amount of the myelin substance. Using these criteria as the basis of distinc-

tion the present writer enumerated the two kinds of the fibers separately, and obtained the following results, which are represented in Table VI.

TABLE VI.

Showing the Number of Fibers, Completely Formed as well as Immature.

Body weight grams.	Total number of the fibers.	Fibers completely formed		Fibers immature.	Percentage of immature fibers.
		Absolute.	Relative.		
VI Cervical					
10.3	1998	1043	1.	955	48%
24.5	2569	2263	2.1	306	12%
68.5	3683	3569	3.4	114	3%
167	4227	4173	4.	54	1.2%
IV Thoracic					
10.3	607	283	1.	424	69%
24.5	683	497	1.7	366	41%
68.5	1420	1259	4.4	161	11%
167	1522	1460	5.	82	5%
II Lumbar					
10.3	723	303	1.	420	58%
24.5	911	678	2.2	233	25%
38.5	1317	1181	3.8	136	10%
167	1644	1565	5.1	79	4%

On examining Table VI we notice in the first place the relative increase in the number of mature fibers between 10.3 and 167 grams is less in the cervical region than in the other two. This means that even at 10.3 grams, there is a larger proportion of the mature fibers in the cervical root than in the other two with which it is compared, and the last column in the table giving the percentage of the immature fibers supports this statement. That is, the cervical root of the 10.3 gram rat contains 48% of immature fibers, while that of the thoracic and lumbar contains 69% and 58% respectively. Further, at maturity there is in the cervical root a smaller percentage of the immature fibers than in either of the others, showing that this root is most completely developed. In the same way, if we compare the lumbar with the thoracic root we find the lumbar is always more advanced in its development; that is, it contains smaller percentage of immature fibers. It thus appears that the roots in the cervical and lumbar regions are more completely

developed than in the thoracic. Just why the cervical and lumbar roots should be so far ahead of the thoracic root in this respect is not at the moment readily explained.

The increase in the total number of fibers in the dorsal nerve roots is only to be explained by the outgrowth of nerve fibers from the spinal ganglion. It follows from this explanation that in the immature rat we should expect to find in a given dorsal root a larger number of the fibers near the ganglion than at the entrance of the root into the spinal cord. On this point, HARDESTY ('99) obtained striking results from counting the fibers in the dorsal roots in the frog. He says "The number of fibers in the dorsal roots decreases from the spinal ganglion towards the spinal cord." This observation has been fully confirmed in his most recent paper ('00) on the same subject. On the other hand, DALE ('00), who counted the number of coccygeal dorsal root fibers in the adult cat at different levels was unable to find such numerical differences in the two levels, one near the cord and the other near the ganglion. He says, "The number of the fibers close to the ganglion is the same as the number of fibers several millimeters from it, both proximally and distally, i. e., none of the medullated fibers given off by the ganglion cells end in the nerve roots close to the ganglion." This observation by DALE has been already explained by HARDESTY as follows: "That DALE's result does not agree with the results previously obtained and here extended is probably due to the fact that the growth of the nervous system of the frog is much slower than that of the mammal. The cat has a fixed period of growth, while the frog, if it does not grow as long as it lives, at least cannot be said not to do so." A similar explanation has been given by the present writer in his previous paper ('01, I) on the finer structure of the spinal ganglion cells in the white rat.

V. THE RELATIONS OF THE NUMBER OF SPINAL GANGLION CELLS TO THE NUMBER OF DORSAL ROOT FIBERS.

TABLE VII.

Showing the numerical relations between the spinal ganglion cells and the dorsal root fibers.

	Body weights grams.	Total number of cells.	Total number of fibers.	Ratios Fibers and Cells.	Ratios Fibers and large cells.
V Cervical	10.3	10996	1998	1:5.5	1:1.2
	24.5	9793	2569	1:4.	1: .93
	68.5	11772	3683	1:3.2	1: .97
	167	12200	4227	1:2.7	1:1.1
IV Thoracic	10.3	7142	607	1:11	1:2.5
	24.5	7068	863	1:8.2	1:2.1
	69.	7611	1420	1:5.3	1:1.6
	167	7406	1522	1:4.3	1:1.2
III Lumbar	10.3	8315	723	1:11.5	1:2.6
	24.5	8200	911	1:9.	1:2.2
	69.	9514	1317	1:7.1	1:2.2
	167	9442	1644	1:5.7	1:2.2

On comparing the total number of cells with the total number of fibers in each of three roots, we note first the most important fact that there is always a great excess of nerve cells in the spinal ganglion. Further, it appears that the number of cells corresponding to each fiber diminishes with the growth of the animal. In the case of the cervical nerve of the 167 gram rat thus falls as low as 2.7 cells for each fiber, which indicates that the increasing number of fibers arises by the gradual maturing of the spinal ganglion cells. If we regard the ratio in the case of the thoracic and lumbar nerves we find that the number of cells for each nerve fiber is at all ages somewhat greater for the lumbar nerve than for the thoracic, despite the fact that in previous tables we have found the lumbar nerve more like the cervical than the thoracic. If now, we compare the number of fibers in each case with the number of large cells, we find that in the cervical region at all ages the number of fibers is approximately equal to the number of large cells, while in both the thoracic and lumbar regions, there are on the average, a trifle over two large nerve cells for each fiber. This

would suggest a constitution of the cervical ganglion which was different from that of the other two, since these two have nearly twice the number of the large cells in proportion to the number of dorsal root fibers. It is possible that this difference is to be explained by the presence of DOGIEL's cells ('97) of second type in the ganglia of the thoracic and the lumbar regions, but DOGIEL's statement would hardly support this as a complete explanation, because he distinctly says that the cells in the second type are comparatively few in number, whereas the relation here given would demand a rather large number of the cells.

The excess in the number of the cells over that of the fibers has been reported by several investigators: HODGE, 1888, counted in the frog the number of fibers in the posterior roots and the number of cells in the corresponding spinal ganglia, and found that one afferent fiber of the frog corresponds in these cases to from 2.45 to 3.26 cells. BÜHLER, 1896, found in the dorsal root of the ninth spinal nerve of the frog (*Rana esculenta*) 680 fibers and in the spinal ganglia about 3500 cells, giving a ratio of 1 to 5; GAULE and LEWIN 1896, found 3173 posterior root fibers in the 32nd. spinal nerve of the rabbit and 20361 in the corresponding spinal ganglia; a ratio of 1:6.4. We see that the excess in the number of spinal ganglion cells has already been observed, but observations here given enlarge our information by showing the excess found in different nerves and at several ages, and, finally, that the ratio diminishes as the animal grows larger.

From the present observations, it is probable that the immature fibers are the processes of some of the large cells, as it will be seen from Table VI that the total number of the large cells exceeds the total number of the fibers. From this fact it is improbable that the immature or smaller fibers in the dorsal root are the processes of the small cells. The excess of the number of the fibers (See Table IV) may be partly explained by the presence of a greater or less number of the apolar cells, in the sense of the early investigators, in the spinal ganglia for the cells of the second type of DOGIEL ('96, '97) (according to

the original describer) are not numerous enough to explain the relations found.

VI. THE SIZE OF THE CELL BODY, THE NUCLEUS AND THE FIBERS AT DIFFERENT AGES.

Twenty of the largest cells with their nuclei, and twenty of the largest fibers, were selected for the measurement in each case. In the case of cell-body and nucleus, three of the largest cells with nuclei from each section, 12 μ thick (10.3 and 24.5 grams), and two of the largest cells from each section, 12 μ thick (68.5 and 167 grams), were selected for the measurement, while in the case of the fibers, twenty of the largest fibers from one section in each case were measured. The following table shows the results thus obtained.

TABLE VIII.

Showing the mean diameters of the cell-body, nucleus and fibers at different ages.

	Body weight Grams.	Mean diameter of cell-body.	Mean diameter of nucleus.	Mean diameter of fibers.
VI Cervical	10.3	39.5	15.4	7.5
	24.5	42.6	15.9	11.6
	68.5	47.9	16.6	13.3
	167	52.7	17.2	13.9
IV Thoracic	10.3	32.	13.	4.8
	24.5	35.6	13.8	7.1
	68.5	40.3	13.9	8.9
	167	47.2	16.5	11.6
II Lumbar	10.3	33.4	12.5	5.1
	24.5	39.9	14.7	8.
	68.5	43.3	15.8	11.3
	167	51.2	17.5	12.

The cell-body is thus seen to be growing constantly from 10.3 grams to maturity. The cervical spinal ganglion contains the largest cells in each stage, the lumbar comes next in rank, while the thoracic shows the smallest size among the three. In the rats between 68.5 and 167 grams, the mean diameter of the cervical spinal ganglion cells enlarges less than that of the lumbar, while the thoracic and lumbar are nearly alike. The comparison of the cell-body and nucleus shows that the

relative increase of the cytoplasm of the cell-body is much more rapid than that of the nucleus, especially in the last stage of the growth—see Table VIII.

VII. SUMMARY.

1. The total number of the spinal ganglion cells remains approximately constant between 10.3 and 167 grams; though individual variations in the number of the cells in corresponding ganglia exist. It can therefore be stated that this number does not increase or decrease with age—Table I.

2. The cervical spinal ganglia contain the greatest number of cells, while the lumbar and thoracic follow in the order named—Table I.

3. Some of the small cells contained in the spinal ganglia are constantly growing, and in all three ganglia, some of them become large cells—Table II.

4. In all the ganglia the relative number of the large and small cells is nearly the same at the same age—Table II.

5. The cervical dorsal root-nerves contain the greatest number of fibers, while the lumbar and thoracic rank in the order given—Table IV.

6. The relative increase of the number of the fibers in the cervical and lumbar nerves is approximately the same, while that of the thoracic shows a more rapid increase than either—Table V.

7. The dorsal root nerves at different regions in 10.3 gram white rat contain a large percentage of immature fibers giving for the cervical 48%, thoracic 69%, lumbar 58%, while in the mature animal the following percentages are found, 1.2%, 5% and 4% respectively. This indicates the greater numerical completeness of the cervical nerve in both young and the adult. The lumbar nerve follows the cervical, while the thoracic shows the least numerical completeness both in the young and nature—Table VI.

8. The number of the cells in the spinal ganglia is always more than twice that of the fibers in the corresponding dorsal root nerves. The ratios between the fibers and cells at 10.3

grams are as follows: Cervical 1:5.5; thoracic 1:11; lumbar 1:11.5; while in the mature form the ratios are 1:2.7; 1:4.3; 1:5.7 respectively—Table VII.

9. The ratios between the fibers and large cells at maturity are as follows: Cervical 1:1.1; thoracic 1:1.2; lumbar 12:2.—Table VII.

10. Excessive number of cells in the thoracic and lumbar ganglia is possibly to be explained in part by the presence of large numbers of DOGIEL's cells of second type in these localities. The explanation is, however, not a complete one—Table VII.

11. The mean diameters of the cell-bodies, nuclei and fibers give the highest figures at the cervical region; the lumbar comes next in rank and the thoracic last. The growth of the cytoplasm is always more rapid than that of the nucleus.

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OBSERVATIONS ON THE MEDULLA SPINALIS OF
THE ELEPHANT WITH SOME COMPARATIVE
STUDIES OF THE INTUMESCENTIA CERVICALIS
AND THE NEURONES OF THE COLUMNA AN-
TERIOR.

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With Plates IX—XIII and one figure in the text.

CONTENTS AND SUMMARY.

I. INTRODUCTION.

1. History of the material.
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Table II.

III. MICROSCOPIC STUDIES.

1. The fasciculus gracilis is well defined in the cervical segments with seemingly a lateral limb extending over the outer periphery of the fasciculus cuneatus.

2. The medullated axones composing the fasciculus gracilis are more compactly bundled and possess a less average caliber than those of the fasciculus cuneatus.

3. Two well defined longitudinal fasciculi occur within the commissura grisea, one on either side of the mid line.

4. These fasciculi probably disappear, as such, in the XVIIIth or XIXth thoracic segment.

5. At the level of the decussatio pyramidum these fasciculi are seen to arise from the decussating pyramidal axones and may therefore be termed *fasciculi cerebro-spinales interni*.

6. The nucleus dorsalis (CLARKE'S column), in addition to the cell-bodies of neurones proper to it, contains numerous longitudinally coursing medullated axones giving it the appearance of a fasciculus rather than a "nucleus."

7. These longitudinal axones of the nucleus dorsalis increase in abundance in passing from the VIIIth to the IInd thoracic segments, and the cell bodies proper to the nucleus seemingly do the same.

8. These axones accumulate in the nucleus dorsalis toward the IInd thoracic segment where they leave the confines of the nucleus, passing obliquely cephalad across the cervix of the columna posterior and enter the funiculi laterales probably to form a fasciculus cerebello-spinalis (direct cerebellar tract).

9. With the departure of these axones the nucleus dorsalis becomes smaller and finally disappears in the Ist thoracic segment.

10. Afferent axones (from radix posterior) enter the confines of the nucleus dorsalis more abundantly in the IInd thoracic segment than in the IVth or VIIIth and probably more abundantly than in any segment caudad to the IInd thoracic.

11. A constant and consistent grouping of the cell-bodies of the columna anterior can not be claimed for the *intumescencia cervicalis*

IV. COMPARATIVE STUDIES.

1. Scope and procedure.

2. Table III, containing the transverse dimensions of the *intumescenciae cervicales* and the average mean diameters of the cell-bodies of the *columnae anteriores* from a series of twelve mammals of diminishing body weights.

3. The diameters of the *medulla spinalis* decrease grad-

ually through the series, but neither the diameters nor the rate of decrease are constantly proportional to the size of the animal.

4. In proportion to the size of the body, the smaller mammal has a very much heavier medulla spinalis than the larger mammal.

5. The area of the transverse section of the medulla spinalis is more expressive of the relation to body weight than the diameters of the transverse section, and the rate at which the areas vary through the series is more nearly proportional to the variations in body weight.

6. The areas of the substantia grisea in transverse section, while in general decreasing gradually through the series, do not vary in accord with the variations in the size of the animals.

7. The average mean diameter of the cell bodies of the columnae anteriores in the intumescenciae cervicales decreases gradually through a series of mammals of diminishing body weight.

8. The volume of the cell-body of the neurones varies more nearly in proportion to the variations in the size of the animals than does the diameter of the cell body.

9. The smaller mammals have the smaller cell-bodies, but in proportion to the size of the body, the smaller mammal possesses a very much larger cell-body than the larger mammal.

10. Through a series of mammals of diminishing body weight, the volume of the entire neurone bears a more constant ratio to the size of the body than either diameter or area, and the variations in the volume of the entire neurone are more nearly proportional to the variations in the size of the body than either the diameter of the cell-body, the volume of the cell-body or the area of the transverse section of the medulla spinalis.

11. Table IV, showing actual and relative areas of substantia grisea and substantia alba in transverse sections from the different mammals, and giving the ratios between these areas and the areas of the cell bodies in section.

12. Through a series of mammals diminishing in body

weight, the area of the substantia alba in transverse section decreases more regularly and more rapidly than the area of the corresponding substantia grisea. Conversely, as the medulla spinalis increases in size through a series of mammals, the increase is more largely due to a more rapid increase of the substantia alba than of the substantia grisea.

13. The ratio of the area of the section of the cell-body to the area of the substantia grisea containing it decreases with considerable regularity through the series, but since the greater area of substantia grisea contains the greater number of cell-bodies, the variations in the ratios are not similar to the variations in the areas of the cell-bodies.

V. BIBLIOGRAPHY.

1. Articles cited.
2. Other literature on the anatomy of the elephant.

VI. EXPLANATION OF ILLUSTRATIONS.

INTRODUCTION.

The material of which the following is a partial description was obtained through the kindness of Dr. CHARLES L. BRISTOL of New York University. Learning that the Barnum and Bailey Company had among their animals at Bridgeport, Conn., a "bad elephant" which it had become necessary to kill, Dr. BRISTOL sought their New York office, was kindly granted the necessary authority and hastened to Bridgeport. He arrived on the scene ten hours after the death of the animal. Circumstances had made it necessary to produce death by strangulation. A great force of men had skinned, disembowelled and laid bare the skeleton of the elephant so quickly as to almost entirely obviate the post mortem rise of temperature which otherwise, in an animal of this size, is such as to render the tissues of its internal organs wholly unfit for microscopic purposes. Thus when Dr. BRISTOL arrived about 7 P. M. he could immediately proceed toward the removal of the tissues desired.

The difficulty of this task may be imagined, especially since it had to be accomplished without injury to the skeleton.

For this reason it was impossible to get the encephalon, as highly as it would have been prized. Furthermore the available time in which to collect the material was so limited that it was even impossible to obtain all of the medulla spinalis. Dr. BRISTOL succeeded, however, in securing a portion of the central nerve axis extending from the calamus scriptorius (severed within the foramen magnum) to the VIIIth thoracic segment. Thus the specimen comprised the major portion of the medulla oblongata, the pars cervicalis and eight segments of the pars thoracalis.

The specimen was divided transversely into pieces 2 to 4 cm. in length and placed in ten per cent. formalin. This fluid was changed twelve hours later and again several times subsequently. Later Dr. BRISTOL forwarded the material to Dr. H. H. DONALDSON, Professor of Neurology in The University of Chicago.

At that time the author enjoyed the privilege of being a Fellow and later an Assistant in the department of Neurology at Chicago, and through the kindness of Dr. DONALDSON was allowed to undertake a description of the material. Most of the work necessary for this discription was done in the Neurological Laboratory under the direction of Dr. DONALDSON.

The elephant was a young male, about twenty-one years of age and of the species *indicus*. He had been treacherous for two or three years, but at this time occurred his first rutting period and he became positively dangerous. He was estimated to weigh about eight thousand pounds and was in excellent vigor at the time of his execution.

Owing to the absence of disease and to the fact that the rapid disembowelling and removal of the vast musculature had practically obviated the injurious effects of post-mortem temperature, it can be assumed with considerable certainty that the tissue obtained was in a normal condition.

The specimen placed at the author's disposal included the caudal end of the medulla oblongata, beginning at the inferior extremity of the ventriculus quartus, and a portion of the medulla spinalis terminating in the VIIIth thoracic segment. Its

extent therefore comprised a portion of the nucleus funiculi gracilis and funiculi cuneati, a portion of the decussatio lemniscorum, the decussatio pyramidum, the segments of the eight Nn. cervicales with the intumescentia cervicalis, and the segments of the seven succeeding Nn. thoracales. Since the elephant possesses nineteen thoracic segments none of the intumescentia lumbalis was included.

The material, being fixed and preserved in formalin, was perfectly suited for the application of the iron-haematoxylin method for the demonstration of the medullated axones and the cell bodies of the neurones.¹ Celloidin sections stained by this method were largely used for the following studies. Those chosen for the illustrations were photographed by transmitted light by means of the large ZEISS projection apparatus. Outline tracings of the photographs were made in certain cases for companion illustrations to the photographs in order to facilitate reference to the parts. In the tracings the positions of structures are indicated, while the actual appearances of the structures are shown in the photographs. Further technique employed will be better given under the discussions involving it.

MACROSCOPIC STUDIES.

A review of the literature has so far disclosed but three papers touching at all upon the medulla spinalis of the elephant. None of these deals with its microscopic anatomy and but one goes with any detail into its macroscopic features. An examination of the literature reveals a greater interest in the reproductive organs of the elephant than in its nervous system. Most of the observations recorded have been within the realm of gross anatomy rather than microscopic. With the hope that it will be of some convenience to others who should undertake studies dealing with the elephant, the author, in addition to the papers cited as touching upon his own observations, has appended a list of other papers found touching upon the anatomy of the elephant.

¹ HARDESTY, Neurological Technique, Method X. *The University of Chicago Press*, 1902.

The study of the specimen should begin naturally with the observation of its macroscopic features. It will be remembered that the author had no opportunity to observe the specimen *in situ*.

OWEN ('68) calls attention to the fact that in the elephant and the whale the cavum subdurale is relatively quite large, but beyond mentioning the general difference between the dorsal and ventral radices he gives no description of the medulla spinalis. The reproductive organs proved of more interest to him.

CLARKE ('58) in dealing with what at that time was considered "The intimate structure of the brain, human and comparative," notes, when touching upon the medulla oblongata, that the "pyramids of the elephant, though not prominent, occur as long and tapering columns."

SPITZKA ('86) in a paper dealing with the comparative anatomy of the pyramidal tract, denies the elephant the possession of "pyramids" individually and makes the general statement that "the *Proboscideae* and *Cetaceae* are characterized by the absence of pyramids in the medulla oblongata and by the consequent exposure and natural approach of the olivary prominences." His definition of pyramids, however, is confined to appearances bearing that name in the human medulla oblongata; i. e., to those columns which emerge at the inferior edge of the pons, bordering the fissura anterior, and mesad to the olivae, and which because of their peculiar shape in the human were given the name "pyramids." Thus his denial of pyramids need not deny pyramidal tracts. Yet in another sentence he states, "The elephant and the porpoise agree in having no pyramid tract—an expression probably of the physiological characters of these animals."

We shall see later that the elephant does possess not only evident pyramids and pyramidal tracts but "crossed pyramidal tracts," though the latter especially, differ considerably from those of man.

KOPSCH ('97) gives the only detailed description of the medulla spinalis of the elephant so far found. It is the special

subject of his paper. His studies however are exclusively macroscopic, no attempt having been made toward the preparation of sections for the study of its finer anatomy.

KOPSCH obtained his specimen from the zoological gardens of Berlin. It comprised the entire medulla spinalis with the exception of the 1st and 2nd cervical segments, which were removed in company with the head. Unfortunately both these and the head were unavailable. The animal was a male *Elephas indicus*. Its age, probable weight and cause of death are not given.

His description begins with the specimen *in situ*. He was able to proceed by removing the neural arches from the columna vertebralis and thus could observe the medulla spinalis enclosed by its meninges and lying in its natural position in the canalis vertebralis. Since the specimen at the disposal of the author had been removed and was even devoid of its dura mater, the author had no opportunity to observe it with reference to its environment. This fact is offered as an additional reason for giving a more detailed review of certain parts of KOPSCH's paper. Also, wherever the author has been able to examine features retained in his specimen and also touched upon by KOPSCH, the observations made upon the two specimens will be compared.

After laying bare the specimen in the canalis vertebralis, KOPSCH noted many fibrous connective tissue bundles joining the dura mater with the wall of the canalis vertebralis. These traversed a relatively wide epidural lymph space which, in man, is occupied by the internal plexus venosus vertebralis and considerable adipose tissue. The latter was absent in the elephant KOPSCH examined.

Next, the dura mater was opened by a median longitudinal slit and laid back so that the medulla spinalis proper could be observed and the relation of its segments to those of the columna vertebralis could be determined.

The cavum subdurale was relatively capacious as OWEN had previously noted. The conus medullaris terminated in the canal of the 1st sacral vertebra and the filum terminale continued

into the os sacrum, the canal of which was not opened. The ligamenta denticulata attained a width of from ten to twelve mm. in the cervical region; in the thoracic and lumbar regions this width varied from six to eight mm. The length of the canalis vertebralis from and including the IIIrd cervical segment to the os sacrum was 175 cm. (The Ist and IInd cervical segments were removed with the head). The length of the corresponding medulla spinalis (dura mater removed) was only 150 cm. There was no evidence of the organ having been stretched or distorted. Its weight was not taken.

The transverse diameter of the canalis vertebralis in the cervical region varied from 65 to 75 mm.; at the level of the thoracic X it was 40 mm. and in the lumbar region the greatest diameter was 60 mm. Corresponding to these diameters, the transverse or lateral diameters of the medulla spinalis were taken at various levels while the specimen was in position. The greatest diameter recorded is 32 mm., and was found in the intumescencia cervicalis. This was reduced to 22.5 mm. in thoracic III and to 20 mm. in thoracic X. Thence the width remained about the same to thoracic XIII where it became 21 mm. The broadest portion of the intumescencia lumbalis had a lateral diameter of 26.5 mm.

KOPSCHE identified 41 pairs of nervi spinales including the first two which had been removed with the head. These he distributed into 8 cervical nerves, 19 thoracic, 3 lumbar, 5 sacral and 6 coccygeal.

The lengths of the segments were taken, measuring from the middle of one segment to that of the adjacent. Cervical V measured 32 mm. in length, cervical VIII 25.3 mm. From cervical VIII the lengths increased in both directions, the greatest being attained in thoracic VII which was 68.7 mm. long. Thence to the conus medullaris the lengths gradually decreased, the segment giving off the last coccygeal nerve having a length of only 4.5 mm.

The author did not attempt measurements of the lengths of the segments of the specimen at his disposal since it had been

divided into short pieces at the time of its fixation and consequently measurements would have involved considerable error.

The specimen described by KOPSCH was removed entire and placed in MÜLLER'S fluid. In this fluid it remained for more than two years. Upon the renewal of its study it was washed in seventy percent. alcohol for about two weeks, then photographed and a drawing made for purposes of orientation. In the further study, various other measurements were made. One set of these deals with the length of the lines, or the areas of pia mater, along which the fila radicularia of the dorsal and ventral radices of the various segments enter or leave the medulla spinalis (zones of entrance and exit). One general difference between the the two radices brought out by these measurements is that the line along which the radix posterior of a given nerve enters the pia is always shorter than that along which the corresponding radix anterior emerges. This, of course, results in a greater space of pia between the fila radicularia of adjacent radices posteriores than between the corresponding radices anteriores. This difference existed very evidently in the Bridgeport specimen and so far as the author is aware is true for vertebrates generally. It is but an expression of the fact that the fila of the radix posterior of a given nerve are thicker and fewer in number than those of its radix anterior. The former result from the division of the radix posterior before entering the pia along the sulcus lateralis posterior. The axones composing them have their origin in definite separated cell masses, the ganglia spinalia, while the fila of the radix anterior have their origin in a continuous column of cell bodies, the columna anterior of the medulla spinalis, and in the process of collecting to form the radices anteriores, emerge through the pia as a greater number of more finely divided filaments and in a more nearly continuous line.

The width or space between the mid line and these lines of entrance and exit of the different radices was observed to uniformly increase in passing from the caudal to the encephalic end of the specimen (Fig. 1, plate IX). This also is a feature common to other species. It but indicates that the ascending

axones in the funiculi posteriores and those descending in the ventral funiculi increase in mass toward the encephalon.

KOPSCH made free-hand traverse sections at different levels and again measured the lateral diameters of the then hardened specimen, and in addition, he measured also the corresponding dorso-ventral diameters. No embedded and stained sections were made and no microscopic examination was undertaken. The measurements included the pia mater spinalis. The breadth of the specimen had been practically unaltered in the process of fixation and hardening. In order to compare the dimensions of the two specimens, the author also measured the two diameters of certain of the segments of the specimen at his disposal. That this comparison may be made and that, at the same time, the dimensions of the segments and their relations to each other may be more readily seen, the author's measurement and the diameters of certain of the segments measured by Kopsch are given in the following tabulated form:

TABLE I.

<i>Segment.</i>	Diameters in mm. KOPSCH.		Diameters in mm. HARDESTY.	
	Lateral	Dorso-ventral	Lateral	Dorso-ventral
Medulla oblongata (Decus. leminsc.)			40	23
Medulla oblongata (decus. pyramid.)			34	17
Medulla spinalis:				
Cervical I			33	17
Cervical IV	32	19	31	18
Cervical VI	28	18	33	19
Thoracic II	23	16	25	16
Thoracic VIII	20	15	20	16
Lumbar I	26	17		
Conus medullaris:				
coccygeal VI	4	3		

TABLE I, showing the lateral and dorso-ventral diameters of certain of the segments of two specimens of the medulla spinalis of the adult elephant. The measurements made by KOPSCH from a specimen fixed in MÜLLER'S fluid are placed in parallel columns to those made by the author from a specimen fixed in formalin. The measurements are reduced to round numbers and include the pia mater spinalis.

KOPSCH'S measurements show the greatest lateral diameter of the intumescencia cervicalis (and of the entire medulla spin-

alis) to be 32 mm. The maximum dimensions are claimed for the IVth cervical segment. Thence the diameters decrease on approaching the pars thoracalis until thoracic V is reached. This segment, not given in the table, had a lateral diameter of 21 mm. and a dorso-ventral diameter of 15.5. From this segment to thoracic XII (also not given) the diameters remained about the same, the lateral varying from 20 to 21 mm., while the dorso-ventral maintained 15.5 to 16 mm. even as far as thoracic XVII. In thoracic XIV, however, the lateral diameter began to increase and in thoracic XIX and lumbar I attained its maximum for the *intumescentia lumbalis*; i. e., a lateral diameter of 26 mm. with a dorso-ventral of 17 mm. Thence began the decrease toward the *conus medullaris*.

The segment of the author's specimen possessing the maximum dimensions was the VIth rather than the IVth cervical. It may be further noted that the lateral diameter of the IInd thoracic segment of the author's specimen is greater than that of the corresponding segment of KOPSCH's specimen. The author's specimen may have been more swollen by the action of the formalin in which it was preserved than had it been preserved in MÜLLER's fluid, but this would not explain the difference shown in the table. There must be some mistake in the statement by KOPSCH that the *intumescentia cervicalis* reaches its maximum in the IVth cervical segment. Although the author's specimen had been divided into several pieces which had to be fitted together in sequence to determine the numbers of the consecutive segments involved, this could be accomplished with no great difficulty and the author is quite positive that the largest segment of the *intumescentia cervicalis* of his specimen was the VIth and not the IVth. Furthermore, of the eleven other mammals dealt with in the comparative studies to be mentioned later, the most enlarged segment of the cervical region was usually the VIth. The largest segment is sometimes the VIIth but is never more cephalad than the Vth. It is possible that KOPSCH, by chance in this one instance, failed to take into account the two segments of his specimen

which had been removed in company with the head and consequently unexamined by him.

It should be mentioned that the segments cephalad to cervical V were more flattened, i. e., the lateral diameter exceeded the dorso-ventral to a greater extent than that of any of the succeeding segments. There was nothing to show that this flatness was not normal. It will be subsequently seen that this feature is also well-marked in the horse.

Fig. 1, plate IX is an outline sketch constructed from the subjoined pieces. Its dimensions were controlled by actual measurements. It shows the relative size of the different segments comprised as well as the transition of the medulla oblongata into the medulla spinalis. The transverse lines indicate the levels at which the diameters were measured for Table I. The levels from which the sections were taken which were used for the illustrations of the internal structure of the specimen, are indicated by the number of the figure showing the sections. The medulla oblongata at the level of the caudal extremity of the ventriculus quartus (calamus scriptorius) and involving the decussatio lemniscorum and a portion of the nuclei giving origin to the lemniscus (Fig. 2, plate X) had a lateral diameter of 40 mm. Its greatest dorso-ventral diameter was 23 mm. However, when taken from the floor of ventriculus quartus the dorso-ventral diameter was only 18 mm. At the level of the decussatio pyramidum (Fig. 4, plate XI) the lateral diameter was 34 mm. and the dorso-ventral 17 mm. These measurements show that the inferior portion of the medulla oblongata is also considerably flattened laterally. KOPSCH's measurements indicate that this feature is maintained, but to a less marked degree, throughout the remainder of the specimen. In the thoracic region the lateral diameter exceeds the dorso-ventral never less than 4 mm., and in the intumescentia lumbalis this excess is even as much as 9 mm. It will be remembered that in the mammals more commonly studied, dog, cat, rabbit, rat, man, monkey, gorilla and orang-outang, an excess of the lateral diameter over the dorso-ventral is marked to a noticeable extent only in the intumescentia cervicalis. Even here for some members of the group,

cat for example, the difference is very slight. In the more commonly studied mammals generally, transverse sections taken from the inferior medulla oblongata, the superior cervical segments, from most of the thoracic and from all of the lumbo-sacral segments, are approximately circular in outline.

The following details may be of interest from the viewpoint of comparative anatomy. The pia mater spinalis averaged about $\frac{1}{2}$ mm. in thickness. The ligamenta denticulata often attained a width of 10 mm. The fila radicularia of the radices posteriores sometimes attained a width of 6 mm. in the cervical region. Those of the thoracic nerves were of course smaller. In section, the fissura mediana anterior seemed rather narrow in proportion to the size of the specimen. The funiculi posteriores are distinctly separated by the septum posterius. The sulcus lateralis anterior is most evident in the pars cervicalis, being indistinct in the pars thoracalis. The sulcus lateralis posterior is well marked along the entire length of the specimen.

KOPSCH's observations upon sections were made entirely upon unstained free hand sections of material preserved in MÜLLER'S fluid. This accounts perhaps for the fact that he failed to note one of the most unusual and striking peculiarities shown in the medulla spinalis of the elephant. On examining a transverse section, better of the pars cervicalis, and especially if the section has been stained by some method differential for the medullated axones, one's attention is instantly called to the existence of two large and well defined fasciculi coursing longitudinally in the commissura grisea. These, occurring one on either side of the mid line, partially split the commissure. They were easily visible to the unaided eye in the formalin preserved material used by the author and in sections stained differentially they become strikingly prominent (*F. c. i.*, Figs. 7 to 12). The nature of these fasciculi will be more closely examined in the microscopic studies to follow. While KOPSCH's illustrations (photographs) show these fasciculi, he does not mention them in his observations. That he did not note them is indicated in his description of the commissura grisea of which he undoubtedly included them as a part. He states that the com-

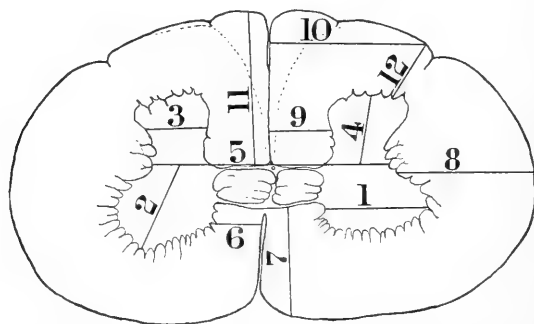
missurae albae posterior and anterior are especially noticeable because of the numerous axones in them, whereas, what he must have taken for such are, instead, the only visible vestiges of the entire commissura grisea proper (see figures) and, while the stained section shows these to contain medullated axones belonging to the commissures mentioned, they are in fact composed largely of connective tissue and neuroglia. KOPSCH further mentioned that the canalis centralis could not be recognized. Because of the presence of the above-named fasciculi the canalis centralis is not situated centrally as is usually observed in other animals, but it could be recognized in the author's specimen (*c. c.*, Fig. 8) when one knew where to look for it.

Figures 2, 4, 7 and 11 are reduced to scale from photographs in which the actual sections were enlarged about ten diameters. They show the relative proportions of four transverse sections taken at the levels indicated in Fig. 1. Each is accompanied by an outline similarly reduced, in which certain of the parts are named.

Comparing the sections with those of the medulla spinalis of man at corresponding levels, attention is drawn to the appearances of the gray figure (substantia grisea) as a whole. While much larger actually, its size in proportion to the amount of substantia alba does not seem so great as in man. The two sides of the gray figure seem widely separated. This latter appearance is due to some extent to the unusual occurrence of substantia alba (fasciculi above-mentioned) in the substance of the commissura grisea, changing its optical appearance from that of other parts of the gray figure. The substantia gelatinosa ROLANDI is greatly developed especially in the cervical and upper thoracic segments (*S. g. R.*, Figs. 5, 8 and 10). KOPSCH describes an extra abundance of substantia gelatinosa in the lumbar segments also. The caput of the columna posterior is separated from the periphery of the section by a comparatively thick zone (LISSAUER's zone?) of substantia alba. It will be remembered that in the smaller mammals the caput often extends to the periphery practically. In the cervical segments, the fasciculus gracilis is so well defined that its boundaries may be seen with the unaided eye.

In addition to the occurrence of the fasciculi cerebro-spinales interni and the resulting peculiar position of the canalis centralis, further macroscopic examination of the sections will prove that in the thoracic segments, the nucleus dorsalis (CLARKE's column) possesses features considerably different from what appears in the medullae spinales of the mammals usually studied. The position of the nucleus in the cervix of the columna posterior is exceedingly well defined in the more cephalad thoracic segments (Figs. 10, 11, 13, 14, 15), and it increases in size in passing from thoracic VIII to thoracic II. A microscopic study of the nucleus is deferred to another section of this paper.

For purposes of comparison and in order to present a more detailed quantitative study of the relative proportions of substantia grisea and substantia alba in the different levels, a series of measurements were made of the various dimensions of each section according to the scheme represented in text-figure 1. The results of these measurements are recorded in Table II. The number enclosed with the title of each entry in the table corresponds to the dimension indicated by the like number in text-figure 1. These measurements were suggested by similar meas-



Text-figure 1—Showing the scheme according to which measurements were made of the various dimensions of the transverse sections of the medulla spinalis of the elephant. The lines in the figure indicate the extent and direction of each measurement and the numbers of the lines correspond to like numbers enclosed in the entries in Table II in which the measurements are recorded for the different sections involved.

urements made by KOPSCH, and the scheme is intentionally the

identical scheme devised by him, so that measurements made from the two specimens may be compared.

KOPSCH tabulates measurements from fourteen of the entire forty-one segments of his specimen. With the addition of KOPSCH's measurements from the intumescentialumbalis, the author has included in Table II only such of the sections measured by KOPSCH as would, by position, compare with such measurements as the author was enabled to make from the material at his disposal. In order to present measurements from a greater number of segments of the localities available, the sections chosen by the author for measurements are from segments intervening between those from which KOPSCH recorded measurements. The author's measurements are placed in parallel columns to those of KOPSCH and are set in heavier type in order to be distinguished.

KOPSCH's measurements were made from photographs of free-hand sections of material which had remained two years in MÜLLER's fluid and then washed for two weeks in 70 per cent. alcohol. The action of the MÜLLER's fluid, in all probability, resulted in a slight increase in the volume of the tissue, which increase was hardly reduced by the subsequent action of the alcohol. The sections were twice enlarged in the photographs and consequently the measurements obtained were reduced one half before recording them in the table.

On the other hand, the author's measurements were made from stained sections of material which had been fixed in ten per cent. formalin, dehydrated with alcohol and embedded in celloidin. Formalin produces a swelling by causing the tissue to take up water, and the subsequent action of the alcohol in dehydration produces an appreciable shrinkage of the tissue, regardless of precautions taken in the process. Measurement of the block while in formalin and then of the section after embedding in celloidin shows that this shrinkage may amount to as much as five per cent. of the diameters of the block while in formalin. How much, or whether at all, the dimensions of the dehydrated formalin material vary from the normal dimensions in the fresh state could not be determined with the material in hand. It is

probable that dehydration results in dimensions less than the normal and it is therefore more than probable that the dimensions of the various parts of the stained sections measured by the author are somewhat less than had the material been subjected fresh to the action of MÜLLER'S fluid.

The author chose stained sections in order to get the dimensions of the various localities more accurately than was possible from the undifferentiated block. Instead of photographs of the sections, the EDINGER *projection apparatus* was used with the aid of transmitted light. With this apparatus the image of the object is thrown horizontally upon the table and directly under the hand of the observer. Distortion is impossible. The sharpness of the image is only a matter of focussing and the required enlargement is easily obtained by adjustment of the apparatus and can be accurately determined by measurement of the image. The projection was done in a dark room. In order to reduce the error, each section from which the following measurements were made, was enlarged exactly ten diameters. The image thus enlarged was sharply focussed on white paper pinned to the table. The outlines of the various parts of the section were then carefully traced out with a sharp-pointed pencil. The outline-drawings thus obtained were removed and the dimensions of the various localities measured in millimeters according to the scheme shown in text-figure I. These then were reduced to the normal dimensions by dividing each result by ten.

The changes in the form of the gray figure and the relations of substantia grisea to substantia alba can be easily read from Table II. In general, the changes which appear in passing through the cervical into the thoracic segments consist in a uniform decrease in all the parts. In the mid-thoracic region the gray figure becomes relatively quite small (see Fig. 11, plate XII). KORSCH'S table shows that it begins to increase again in thoracic XV. Two series of changes can be read in the parts of the gray figure; viz., changes in size and changes in position. The latter are indicated in the measurements of the width of the anterior and posterior funiculi (measurements 6, 9 and

10). The columnæ anteriores and posteriores become more sagittally placed in the thoracic segments because of the decrease in the amount of substantia alba in these funiculi, and

TABLE II.

	Cervical I	Cervical IV	Cervical VI	Cervical VIII	Thoracic II	Thoracic III	Thoracic IV	Thoracic V	Thoracic VIII	Thoracic XIX
<i>Substantia grisea.</i>										
Columna anterior:										
(1) Greatest thickness	3.3	5.5	6.0	4.0	2.5	1.0	1.0	1.0	0.9	5.3
(2) Depth	6.0	5.0	5.7	5.0	3.8	3.5	3.5	2.8	4.0	4.0
Columna posterior:										
(3) Thickness	3.9	2.5	3.3	2.8	3.3	1.8	1.5	1.5	1.3	2.8
(4) Depth	6.5	5.0	4.2	4.0	3.0	3.3	3.5	4.0	2.5	5.3
(5) Total width	14.0	12.5	13.3	11.0	9.4	5.8	6.3	4.3	4.5	14.0
<i>Substantia alba.</i>										
Funiculi anteriores:										
(6) Width	3.5	3.0	2.9	3.5	2.5	2.3	1.6	1.3	1.2	2.3
(7) Depth	7.5	7.5	6.4	8.0	7.0	6.5	7.4	6.0	7.1	7.0
Funiculi laterales:										
(8) Width	9.5	8.5	8.3	7.8	7.8	8.5	8.3	8.3	7.0	5.5
Funiculi posteriores:										
(9) Width in neck	4.5	3.8	3.5	2.5	2.4	1.8	1.8	1.3	1.4	3.3
(10) Width at summit	11.2	9.8	8.4	7.5	6.3	6.3	6.3	6.5	6.6	8.0
(11) Depth	7.0	9.5	9.0	7.8	7.0	7.0	6.2	7.5	6.5	8.0
(12) Width, LISSAUER'S Zone	2.6	3.5	3.8	3.6	2.8	4.0	3.7	4.0	4.0	1.5

TABLE II. Giving the dimensions of the parts indicated as found in transverse sections from different segments of the medulla spinalis of the elephant. The segments are noted in the headings of the columns. The measurements are recorded in millimeters. The numbers enclosed with the different entries correspond to like numbers in text-figure I, and thus indicate the locality and direction of the dimension recorded. Measurements recorded in heavier type are those made from the author's specimen. All others are taken from KOPSCHE's table of similar measurements (loc. cit.). Thoracic XIX is included from KOPSCHE's table as the segment possessing the largest dimensions of any in the intumescentia lumbalis.

the columna anterior becomes thinner chiefly because of the absence of the columna lateralis (lateral horn). KOPSCHE's measurements show that, in the intumescentia lumbalis, it becomes almost as thick as in cervical IV, though it still maintains a more sagittal position. The slight increase in the width of the anterior and posterior funiculi in the lumbar segments is interpreted as due to the greater abundance of fasciculi proprii

(ground bundles) naturally accompanying the increase in the abundance of substantia grisea. In cervical I the columna anterior is thinner than in the more caudal cervical segments, but does not acquire a more sagittal position because of the greater accumulation of descending (?) axones here than at levels caudad to this segment. Here the depth of the columna anterior is greater even than cervical VI. Its less thickness is due to the absence of the columna lateralis, which is very evident in the *intumescentia cervicalis* where it contains the cell-bodies of motor neurones supplying the anterior extremities of the body.

The columnae posteriores are, as is to be expected, widely deflected from the mid-line in cervical I, due chiefly no doubt to the great width of the funiculi posteriores (*gracilis* and *cuneatus*) or the great accumulation of ascending axones, but in part also due to an increase in the *fasciculus proprius dorsalis*. The *caput columnae posteriores* is also thicker in cervical I than at any other level, owing to a great abundance of substantia gelatinosa ROLANDI. This substance is also very abundant in the sections involving the medulla oblongata (Figs. 2 and 3). At the *decussatio pyramidum* (Fig. 3) the cervix is apparently thinner because of the greater number of axones coursing in it, producing the appearance of *processi reticulares*, but in this section the columnae anteriores appear much as in cervical I, only having less depth. In the thoracic segments, especially, the distance of the *caput columnae posterioris* from the periphery of the section (width of LISSAUER's zone) appears relatively great (Fig. 11) as compared with the condition in the more frequently studied specimens. According to KOPSCH this distance becomes less in the lumbar segments, a condition which must be explained by the increase in the depths of the columna posterior, for the axones composing LISSAUER's zone (axones of afferent neurones of the first order) must enter more abundantly here from the larger radices posteriores than in the thoracic segments.

The total width of the gray figure (measurement 5) decreases with tolerable regularity from cervical I to the mid-thoracic segments. According to KOPSCH's table, it begins to in-

crease again in thoracic XII, and in the intumescencia lumbalis, attains dimensions nearly equal to those in the cervical segments, and then rapidly decreases into the conus medullaris. These variations are little more than an expression of the variations in the lateral diameter of the specimen. The increased fasciculi proprii attendant upon the greater amount of substantia grisea in the lumbar segments account almost wholly for the increase of substantia alba in the intumescencia lumbalis, for naturally the axones of longer course must be less abundant here than in the thoracic segments, though they may not be so compactly bundled. However, that the funiculi posteriores (measurements 9 and 10) have a greater width in the lumbar than in the mid-thoracic segments may be explained as not only due to the increased fasciculi proprii dorsales, but to some extent as due to the presence of a greater number of the shorter descending divisions of the entering afferent axones attendant upon the larger lumbar radices posteriores, and also to the consequent greater number of collateral branches.

That the funiculi posteriores are wider in the cervical than in the lumbar segments must be almost entirely due to the necessarily greater bulk of cerebro-spinal axones ascending in them, for the fasciculi proprii attendant upon the abundance of substantia grisea and the descending branches of afferent axones and their collaterals can hardly contribute more to the increase of these funiculi than they do in the lumbar segments.

It is interesting to note that the space attributed to the funiculi laterales (measurement 8) does not vary so much at the different levels as would be expected from our knowledge of the components of these funiculi in the medulla spinalis of man and certain other mammals. The absence of a more graded decrease may be explained to some extent by the, at least, partial absence from these funiculi of the fasciculus cerebro-spinalis lateralis (crossed pyramidal tract). An attempt will be made to show that this fasciculus runs instead in the commissura grisea. A glance at figures 7, 14, 10, and 11 (*F. c. i.*) will convince one that the fasciculus occurring here decreases gradually in passing through the cervical and thoracic segments.

It will be shown also that the peculiar appearance of the nucleus dorsalis (CLARKE's column) may suggest the partial absence of another variable from the funiculi laterales.

MICROSCOPIC STUDIES.

Examination of a section taken from the intumescencia cervicalis, even with the unaided eye, will reveal two prominent features, one of which is peculiar. First, the fasciculus gracilis is exceedingly well differentiated (*F. g.*, Figs. 7 and 8). Its relative depth is fully as great as in the human specimen at this level. Further, at the periphery, it seemingly sends a lateral limb over the outer periphery of the fasciculus cuneatus. A microscopic examination shows that the axones composing the fasciculus gracilis are more closely bundled, and micro-measurements prove that they have a smaller average caliber than those composing the fasciculus cuneatus. If the fasciculus gracilis has the meaning here it has in other mammals, its axones being more compactly accumulated may perhaps be the result of the fact that, arising from the ganglia spinalia of the inferior segments, they have run a longer course and become in consequence more individually associated and more closely arranged than those of the fasciculus cuneatus.

Second, on examining a transverse section from the cervical segments especially, one's attention is immediately drawn to an unusual feature. The two longitudinal fasciculi mentioned above as occurring in the commissura grisea are both appreciable and well defined. They are placed, one on either side of the mid-line, and tend to divide the commissura grisea into a dorsal and a ventral lamina (*F. c. i.*, Figs. 7 and 8). They course more in the ventral portion of the commissura grisea, however, for the canalis centralis is contained on their dorsal side. Figure 9 is a detail from Figure 7, and is especially intended to show this region of the section. Under the microscope this dorsal portion of the commissure appears to be composed largely of neuroglia (substantia gelatinosa centralis). No nerve cell bodies are to be observed in it. However, it is traversed by quite a number of medullated axones. These are con-

sidered as representing the commissura alba posterior, passing from the dorsal portion of one side of the gray figure to the other side. The ventral portion of the commissura grisea is subdivided by the above longitudinal fasciculi into a number of laminae, or perhaps trabeculae, and is so displaced that the more ventral of these often come in contact with the pia mater of the fissura mediana anterior. These ventral laminae seemingly contain little or no neuroglia but are rich in white fibrous connective tissue much of which is probably derived from the pia direct. Medullated axones are much more abundant in these than in the dorsal lamina and, so far as may be judged from WEIGERT preparations, they are axones arising from cell-bodies situated in the columnae anteriores. They may then be considered as representing the commissura alba anterior (*C. a. a.*, Fig. 8). They may be traced coursing in the laminae, or trabeculae, from each column anterior and are so numerous that in the mid-line quite an apparent decussation is produced.

For a more detailed study of the fasciculi coursing longitudinally in the commissura grisea, attention is first called to their gradual decrease in passing from the cervical through thoracic segments. This decrease may be observed by comparing Figures 9, 14, 10, and 13 in the order named. These are details from cervical VI, and thoracic II, IV, and VIII and are reduced to scale from photographs. From an examination of KOPSCH's photographs it appears probable that these fasciculi have entirely disappeared in thoracic XVIII.

To determine the nature of these fasciculi attention is next invited to Figures 2 and 3. These figures show the arrangement of the parts in a transverse section of the medulla oblongata involving the decussatio lemniscorum (*D. l.*), the inferior tip of the oliva (*O. i.*), the radix and nucleus *N. hypoglossi* (*N. N. h.*), and the nuclei of the funiculi posteriores (*N. f. g.* and *N. f. c.*). The pyramids (*P*), while not forming so prominent a feature as in the human specimen, for example, are yet sufficiently prominent in the elephant to be easily discerned and in transverse section are clearly marked out, even separated by an ingrowth of connective tissue.

Figures 4 and 5 represent a section passing through the beginning nucleus fasciculi gracilis (*N. f. g.*) and through the decussatio pyramidum (*D. p.*). Figure 6 is a detail showing the ventral portion of Figure 4. The pyramids (*P*) are not so prominent as in Figure 2 since many of the axones composing them have passed dorsalward in the process of decussation. The fissura mediana anterior is partially obliterated by the decussation and the pia mater sends connective tissue trabeculae into the midst of the decussation. Attention is especially called to the fact that there is no indication of the decussating pyramidal axones passing over to the funiculi laterales of the opposite side. The columna anterior (ventral horn) is intact and, with the exception of having less depth, its form here is very similar to its form in cervical I and II, or well below the decussatio pyramidum. In those specimens, human especially, in which the decussating axones are known to pass over into the funiculi laterales of the opposite side, one of the most striking features of a section at this level is the almost entire obliteration of the columna anterior. In order to attain their lateral position in the fasciculus cerebro-spinalis lateralis (crossed pyramidal tract), the axones pass through the columna anterior in such abundance and so disperse its substance that only its most ventral margin remains intact. The sections show that this is not the case in the elephant. Under the microscope the pyramidal axones are seen to decussate abundantly, but instead of passing through the columna anterior to assume a more lateral position, they remain mesial to the columna anterior and at first go to form fasciculi in the more dorsal portions of the funiculi anteriores. Very few, if any, seem to penetrate the substantia grisea at all. Numerous trabeculae from the columnae anteriores pass into and through the intervening fasciculi and these trabeculae contain medullated axones. Some of these axones are, perhaps, contributed from the fasciculi in question, but of these it can not be said that an appreciable number pass through the columna anterior to the lateral funiculi. As pyramidal axones, many would terminate within the substantia grisea. Many of the axones found in the trabeculae, arise, no

doubt, in the substantia grisea of one side and cross over to the other side as components of the commissura alba anterior as in the medulla spinalis. In passing into the medulla spinalis, the fasciculi seen to arise from the decussatio pyramidum become more compactly bundled and the trabeculae become condensed into the commissura anterior as found in lower segments. As compared with the more common mammals, this commissure appears displaced ventrally, an appearance resulting from the accumulation of these pyramidal axones on its dorsal side. The result is consequently that two longitudinal fasciculi are isolated, one on either side of the mid-line and so enclosed as to appear situated within the commissura grisea between its anterior and posterior commissurae albae.

Therefore, it is assumed that the internal or enclosed fasciculi found in the medulla spinalis of the elephant are composed of crossed pyramidal axones, and thus each may be classed as that fasciculus which in man is situated laterally and which is called "fasciculus cerebro-spinalis lateralis" or crossed pyramidal tract. This being true, this internal fasciculus of the elephant may be designated as "fasciculus cerebro-spinalis internus" (*F. c. i.*, Figs. 5, 8 and 12). Its isolation is the result of its position.

In having its crossed pyramidal tracts situated mesially instead of laterally the elephant is not wholly unique. For the purpose of making some comparative studies of sections from the intumescencia cervicalis, material was obtained from several of the common but infrequently studied mammals. In addition to the sections from the required cervical segment, sections were also made from the medulla oblongata of several of these. Among them was the horse. The medulla oblongata of this animal proved a very interesting subject in itself. Its description will not be taken up here further than to say that the mass of pyramidal axones seems great, and that their decussation in the medulla oblongata is so marked and localized as to entirely obliterate all suggestion of the form of the columna anterior. Yet it appears from a study of several serial sections that all of the decussating axones do not pass over into the funiculi later-

ales. Certain of them remain nearer the mid-line just ventral to a seemingly attenuated commissura grisea. In sections inferior to the decussatio pyramidum where the columnae anteriores have their natural form, these axones collect as fasciculi much smaller but similar to the fasciculi cerebro-spinalis interni of the elephant. They become bounded on the ventral side by the commissura alba anterior in the same way as in the elephant. However, they gradually decrease through the superior cervical segments (quite long in the horse) and disappear in the intumescentia cervicalis where the commissura grisea assumes the more familiar form of having its two commissurae albae undisturbed by the presence of an unusual amount of medullated axones between them.

Furthermore, it appears not wholly unusual for the crossed pyramidal axones to course nearer the mid-line than in the lateral funiculi, though not on the ventral side of the commissura grisea nor in it. LENHOSSÉK ('95) states that in the guinea pig, the mouse, and the rat, the crossed pyramidal tracts course in the ventral portion of the funiculi posteriores. In the rabbit and hare (rodents also) and in the dog, cat, etc., these fasciculi course in the lateral columns exclusively. In all of these the pyramidal decussation as such is complete. In some cases uncrossed pyramidal axones course in the funiculi laterales. A ventral uncrossed pyramidal bundle (fasciculus cerebro-spinalis anterior) appears, according to LENHOSSÉK, a prerogative of man and probably of the anthropoid apes. However, in fifteen per cent. of the cases it is absent in man. There were no means, of course, of determining whether the decussation is complete or not in the elephant.

It has already been noted from the measurements in Table II that the thickness of the funiculi laterales varies less than any other feature in sections taken from the various segments of the elephant. While this laterally disposed substantia alba is abundant throughout the specimen, contributing to its comparatively excessive lateral diameter, its approximate constancy indicates the absence of very variable components. The pyramidal tract is a variable and its presence in the lateral funiculi

would tend to produce a more marked increase in their thickness in passing cephalad. From what has just been shown, it is hardly probable that the lateral funiculi are largely contributed to by pyramidal axones. In fact, these fasciculi are relatively most bulky at the level of the decussatio pyramidum (Fig. 4) where, if they were increased by the addition of a crossed pyramidal tract, they would only be in the process of receiving this addition and would therefore, instead of being thicker, be less bulky than at the levels immediately below. The width of the funiculi laterales in the section shown in Figure 4 is 10 mm., while at the 1st cervical segment, Table II shows it to be 9.5 mm. It will be remembered that a transverse section of the human medulla oblongata is approximately circular at the level of the decussatio pyramidum. The same will be recalled for other specimens in which, at this level, the pyramids, conducive as such to a greater dorso-ventral diameter, are in the process of crossing over to increase the funiculi laterales and the lateral diameter of the specimen.

In passing toward the cervical region, Table II shows that in the more cephalic thoracic segments there is a tendency toward a slight increase in the width of the funiculi laterales. This increase is no doubt due, at least in part, to an increase in the abundance of the fasciculus proprius lateralis (lateral ground bundle) attendant upon the increase in the substantia grisea which begins in these segments. But in addition to this, the peculiar appearance of the nucleus dorsalis (CLARKE's column) lends a partial explanation for this increase in the funiculi laterales in the first thoracic segments. Our present knowledge of this nucleus is to the effect that the neurones whose cell-bodies are situated within it receive their stimuli from afferent axones, and collaterals of such, which enter the medulla spinalis by way of the radix posterior, and that the majority of the neurones of the nucleus send their axones over to the lateral periphery of the same side where they join the ascending fasciculus cerebello-spinalis (direct cerebellar tract). A study of the sections goes to show that in the elephant the nucleus dorsalis contributes

most abundantly to the funiculi laterales in the IIInd thoracic segment.

Figures 13, 10, 14, 15 and 16 show what is thought to be the behavior of the axones arising in the nucleus dorsalis. Figure 13 is a detail from Figure 11 (Thoracic VIII). Figure 10 is a similar detail from a section taken through thoracic IV. Figure 14 represents the central region of a section passing through the caudal portion of thoracic II. Figure 15 shows one half of the same area of a section through thoracic II but about 1 cm. cephalad to Figure 14. Figure 16 is an outline drawing from a section taken between Figure 14 and Figure 15 and comprises a reconstruction of the region of the nucleus dorsalis, representing an approximate summation of the behavior of the axones entering (*A*) and leaving (*C*) the nucleus dorsalis (*Nd.*) as determined from a study of sections intervening between those represented by Figures 14 and 15.

Sections taken through the cephalic end of thoracic II show the nucleus rapidly diminishing in size. It disappears in thoracic I and, consequently, is absent in cervical VIII and cervical VI (Fig. 7).

It is unfortunate that the segments caudad to thoracic VIII were not available from which to determine the behavior of the nucleus dorsalis to its caudal termination.

A careful examination of the section through thoracic VIII (Figs. 11, 12 and 13) shows the nucleus dorsalis [*N.d. (C.c.)*] not so distinctly defined as at more cephalad levels, and that it contains numerous transversely cut (longitudinal) axones in addition to cell bodies peculiar to the nucleus dorsalis or CLARKE'S column. In thoracic IV (Fig. 10), four segments or about 24 cm. cephalad to the level of Figure 13, the nucleus has become larger and very distinctly defined. Under the microscope this distinct definition is seen to be due to an increase in the number of medullated axones coursing longitudinally in it, giving it the nature of a fasciculus rather than a nucleus. It is even enclosed by a capsule of connective tissue.

Examination of the sections caudad to thoracic II reveals very few if any axones which can be confidently considered as

leaving the nucleus to pass over into the funiculi laterales. In thoracic IV (Fig. 10) the sections show afferent axones from the radix posterior (some perhaps collaterals of such from the funiculi posteriores) entering the nucleus dorsalis more numerous than in thoracic VIII.

In thoracic II a change occurs and with surprising rapidity. Figure 14 is given to show the beginning of this change. Numerous afferent axones are seen to enter the nucleus dorsalis of both sides of the section. The nucleus on the right of the figure shows the first indication of the seemingly sudden departure of axones to cross over the cervix of the columna posterior into the funiculi laterales. A few millimeters cephalad to Figure 14, the number of these axones increases and their nature and destination become more decided. In Figure 15, about 1 cm. cephalad to Figure 14, the process is at its maximum, while the nucleus has decreased in size. Adjacent sections show that in the process of leaving the nucleus, these axones pass obliquely cephalad so that in a transverse section their entire course is not shown. An attempt is made to show their general course in Figure 16 which is a summation of the appearances of the nucleus and its vicinity as observed from sections intervening between Figures 14 and 15. The nucleus (*Nd.*) is shown in its greater size and double contour revealed in its section a few millimeters caudad to Figure 15 (see Fig. 14). The axones (*C*) considered as arising from cell-bodies situated along the extent of the nucleus, cross the cervix of the columna posterior and enter the lateral funiculi, where, coursing obliquely, they are lost. From our knowledge of their behavior in other mammals, we are led to assume that they finally accumulate in the dorso-lateral periphery to form the fasciculus cerebello-spinalis (direct cerebellar tract).

The figures also show an increase in the number of afferent axones entering the confines of the nucleus dorsalis. These, derived from the radix posterior, course ventrally along the mesial border of the columna posterior and, in the cervix, turn toward the nucleus (Figs. 14 and 15 and A., Fig. 16). Their increase in number as compared with sections from more caudal

segments is to be expected from the greater size of radices posteriores of the more cephalad thoracic segments. All of the afferent axones, so disposed, do not seem to enter the confines of the nucleus directly. Many of them seem first to collect in minute fasciculi on the dorsal side of the nucleus (*D*, Fig. 16). These minute fasciculi disappear in the more caudal sections and it is assumed that they are axones passing caudad to enter the nucleus at other levels. No doubt many of the axones observed as coursing longitudinally in the nucleus are of this type.

In a recent description of the medulla spinalis of the orang-outang (*Satyrus niger*) FIGUEIREDO-RODRIGUES ('01) noted many medullated axones coursing in the nucleus dorsalis. In his figures these appear more numerous than is usually described for man. He describes them as varying in amount at different levels and considers them as derived from the radix posterior. He describes but one section from the thoracic region and does not state from what segment this is taken. He goes into little detail in dealing with this part of his specimen and, with reference to the axones from the nucleus dorsalis, simply makes the general statement (p. 441) that these pass out in the direction of the fasciculus cerebello-spinalis. This author further shows that the nucleus dorsalis of the orang-outang acquires its greatest number of cell bodies and contains the greatest number of transversely cut axones in the IIIrd lumbar segment. This is interesting because, in man, the nucleus is usually described as extending only between this segment and the VIIth cervical, and therefore its caudal termination usually occurs in the IInd lumbar. His figures, however, show that in the orang-outang the most enlarged portion of the intumescencia lumbalis occurs in the VIth lumbar segment, instead of in the Ist or IInd as is usually the case in man. For the elephant, KOPSCH describes the most enlarged portion of the intumescencia lumbalis as occurring in the caudal end of the XIXth thoracic segment.

FIGUEIREDO-RODRIGUES describes the axones coursing in the nucleus dorsalis of the orang-outang as being collected around the periphery of the nucleus, appearing in transverse

section as a ring enclosing the cell-bodies of the nucleus within its center. For man, the much fewer axones of this type coursing in the nucleus are described, see BARKER ('99), as being split into two divisions, one of which courses at each side of the nucleus. Neither of these conditions is true for the elephant. Here the medullated axones predominate greatly over the cell-bodies and prevail equally over the whole domain of the nucleus forming a compact fasciculus (Figs. 10, 14, and 15) in which cell-bodies are sparsely scattered.

The number of the cell-bodies composing the nucleus dorsalis of the elephant was found relatively small in all of the sections examined. The number, however, was found to be greater in thoracic IV than in thoracic II and greater even than in thoracic VIII. The counts involved only the cell-bodies of the large approximately spherical type supposed to be peculiar to the nucleus dorsalis. The average number per section was determined for each of the above segments. The sections were 30 micra thick and, to avoid twice counting, only those cell-bodies containing nucleoli were counted. The counts involved the nucleus dorsalis of the two sides of four sections from each of the three segments. In other words, for each segment the cell-bodies in eight sections of the nucleus were counted and the average number determined for each section of 30 micra. The average for thoracic VIII was 3 cell-bodies per section of the nucleus; for thoracic IV, 8 cell-bodies, and for thoracic II, 5 cell-bodies. Though the counts are inadequate to base conclusions upon, they suggest that the number increases from thoracic VIII to thoracic IV or III and then decreases as the nucleus decreases.

The average mean diameter of the cell-bodies counted was found to be 43.5 micra. It will be seen later that this is little more than half the average mean diameter of the large cell-bodies of the columna anterior of the intumescentia cervicalis.

It should be mentioned that in addition to these large approximately spherical cell-bodies which were counted and measured, each section of the nucleus dorsalis contained quite a number of much smaller cell-bodies. These were of the small stellate and fusiform type scattered abundantly throughout the

whole cervix columnae posterioris and dorsal portion of the columna anterior and were considered as belonging to this type (central or intermediate neurones) rather than as peculiar to the nucleus dorsalis. These may be concerned with the neurones of the nucleus dorsalis proper, but only as neurones whose axones are of short course and serve as association and commissural pathways for the segment containing them. As such, they were not included in the counts.

From the foregoing observations upon the nucleus dorsalis of the elephant the following conclusions are advanced :

1. The afferent axones from the radices posteriores enter the nucleus dorsalis more abundantly in the caudal end of the IInd thoracic segment than in any segment between this and the VIIIth thoracic inclusive.

2. That some of these afferent axones pass caudad to terminate in the nucleus dorsalis at other levels.

3. That, in addition to the above mentioned axones and the cell-bodies proper to it, the nucleus dorsalis contains many other longitudinally coursing medullated axones giving it the appearance of a compact fasciculus rather than a nucleus.

4. That these latter axones increase in abundance in passing from thoracic VIII to thoracic II and that in all probability the cell bodies peculiar to the nucleus do the same.

5. That in the caudal portion of thoracic II, there is a sudden disposition on the part of the axones coursing in the nucleus dorsalis to leave its confines, passing obliquely cephalad across the cervix of the columna posterior to enter the funiculi laterales, probably to form the fasciculus cerebello-spinalis.

6. That with the departure of these axones the nucleus dorsalis becomes smaller, its cell bodies fewer, and that it disappears in the Ist thoracic segment.

As to the grouping of the cell bodies in the columna anterior, little can be said. In other animals the grouping generally described is more evident in the cervical segments. Here for the elephant, in the same segment, some sections will show a tendency toward grouping not displayed in others. In general it may be said that the cell-bodies are very numerous but that

they are not distinctly distributed in groups such as are, for example, described by WALDEYER ('88) for the medulla spinalis of the Gorilla. Sometimes in the same section the cell-bodies will be more distinctly grouped on one side than on the other. In the section from cervical VI (Fig. 7), on the right side of the figure the cell-bodies of the columna lateralis (lateral horn) are gathered into the ventro-lateral, the two postero-lateral and the medio-lateral groups quite distinctly, while on the other side, no such grouping is apparent. In the latter, these cell-bodies, supposed to send motor axones to the muscles of the fore limb, are quite evenly scattered over the whole area. The ventral group, almost absent on the right side of the section, is in other sections quite evident. The mesial group, in both its ventro- and postero-divisions, can in some sections be determined, while in others the cells composing it are few and scattered along the entire mesial border. This group, innervating the muscles of the vertebral column is, of course, represented along the entire medulla spinalis, and is practically alone present in the narrow columna anterior of the mid-thoracic segments such as is shown in Figure 11.

In general the cell bodies of the columna anterior are noticeably large. Measurement of the ten largest found in three sections of the intumescencia cervicalis including and adjacent to that shown in Figure 7, gave an average mean diameter of 84.4 micra.

COMPARATIVE STUDIES.

The above observations upon the medulla spinalis of the elephant suggested the making of certain comparisons between it and that of other mammals. Toward this end material was prepared in a similar way from eleven other animals. Thus, including the elephant, the following studies will deal with a series of twelve mammals.

It was thought that the comparisons might be of more interest if the series included mammals with body weights varying from the largest to the smallest. Despite many efforts the series is not so satisfactory in this respect as could

be desired. No opportunity was offered to obtain the medulla spinalis of the whale, the largest of the living mammals, and likewise all efforts have so far failed to obtain a specimen of the small shrews (Soricidae) some of which (*Sorex personatus*, perhaps) are among the smallest of North American mammals, with the probable exception of the much more rare *Peromyscus taylori* of southwestern Texas. Failing to get a specimen of *Sorex personatus*, the small brownish gray bat, *Atalapha cinerea*, had to be used instead. Therefore, the series begins with the elephant and ends with the bat, and the intermediate members were chosen with as much regard to a gradual variation in body weight as convenience in obtaining them would allow. Only adult animals were used. The position of an animal in the series was determined by an estimation of the normal adult body weight of the species. In the case of the dog, where the numerous varieties afford a wide range in the adult body weight, the specimen chosen was a hound both because of the medium size of this variety and because its body weight would fall in the series about mid-way between that of the monkey, where there was no choice at the time, and that of the hog employed. A hound was thought to be the best of several varieties of similar size, because in such, the proportion between body weight and nervous system is perhaps more nearly normal for the species, *Canis familiaris*, than in other varieties and especially better than in either a very small or very large variety of dog. It is well known that in the small varieties, obtained by cultivation and artificial selection, the central nervous system is exceptionally large in proportion to the size of the body, while, on the other hand, the size of the large varieties consists more in an over-development of the muscular and osseous systems than in an attendant increase in the volume of the central nervous system.

Since it was impossible to get the intact weight of certain members of the series, none of the others were individually weighed. In fact their individual weight was not considered of so much importance. The position of each in the series was rather determined by an estimation of the average weight of its

kind. Considering excessive fat as abnormal, this could be easily done in so limited a series. For example the variety of cat used was appreciable larger as an adult than the adult white rabbit. The ox (a large beef steer) has a larger body than the average horse (an ordinary farm horse). The subject from which the human material was obtained was estimated to weigh 160 pounds in health, an approximately average weight.

The comparative studies here undertaken will deal with transverse sections taken from one segment only of each of the specimens. A comparison of the same segment throughout the series ought to give most of the variations of interest which would be shown by the much more tedious comparison of the various segments throughout the series.

The segment chosen for the purpose was that segment of the *intumescencia cervicalis* which, in each case, possessed the greatest mean diameter. In other words the sections compared were taken transversely through the largest portions of the cervical enlargements. Usually, this was the VIth cervical segment. Beyond a comparison of the lateral and dorso-ventral diameters of this largest cervical segment of each specimen, no attempt is made to show differences in shape and general topography of the sections and no illustrations are given of the sections from the different animals.

The studies will include only the following comparisons :

1. Dimensions of the sections.
2. Total areas of the sections.
3. Areas of the *substantia alba* in section.
4. Areas of the *substantia grisea* in section.
5. Ratio of area of section of *substantia grisea* to total area of section.
6. Ratios between the areas of the *substantia grisea* and *substantia alba*.
7. Average mean diameters of the largest cell-bodies of the *columnae anteriores*.
8. Volumes of the neurones whose cell-bodies are situated in the *columnae anteriores*.

9. Ratio between the area of the section of the average cell-body and the total area of the section.

10. Ratio between the area of section of average cell-body and area of section of substantia grisea containing it.

A trustworthy determination of the caliber of the medullated axones composing the radices anteriores of the segments compared could not be obtained from the sections in all the cases for their preparation was neglected at the time the material was obtained. In a few instances such as could be determined will be made use of.

The data to be used in making the above comparisons are accumulated in the following Table:

TABLE III.

The animal. Arranged according to normal body weight	(1) Average mean diameter of 10 largest cell-bodies in 3 sections, μ	(2) (3) Diameters of sections		(4)	(5)	(6)	(7)
		Lateral mm.	Dorso-ventral mm.	Mean diameters of sections, mm.	Total areas of sections, sq. mm.	Areas of total gray figure, sq. mm.	Areas of gray figure ventral to dorsal border of commissura grisea, sq. mm.
Elephant (<i>Elephas indicus</i>)	84.4	30.0	17.0	23.5	432.6	76.5	52.9
Ox (<i>Bos taurus</i>)	65.0	20.0	14.0	17.0	207.8	29.7	20.5
Horse (<i>Equus caballus</i>)	61.9	20.0	10.0	15.0	211.4	34.3	22.3
Man (<i>Homo sapiens</i>)	58.0	16.5	10.0	13.2	132.3	21.8	15.6
Hog (<i>Sus scrofa</i>)	55.5	12.5	8.5	10.5	83.9	14.1	7.9
Dog (<i>Canis familiaris</i>)	58.7	8.0	6.0	7.0	29.5	8.9	5.7
Monkey (<i>Cynocephalus babuin</i>)	54.0	8.0	5.0	6.5	29.3	9.2	6.2
Cat (<i>Felis domestica</i>)	53.5	7.5	6.0	6.7	29.5	10.5	4.5
Rabbit (<i>Lepus cuniculus domesticus</i>)	39.2	5.5	4.0	4.7	15.2	4.0	2.7
Rat (<i>Mus rattus, albus</i>)	34.7	4.0	2.5	3.2	5.9	2.4	1.3
Mouse (<i>Mus musculus, albus</i>)	27.4	2.0	1.5	1.7	2.8	1.4	0.8
Bat (<i>Atalapha cinerea</i>)	30.6	1.8	1.1	1.4	1.7	0.9	0.7

TABLE III. Giving the respective dimensions and areas of transverse sections taken from the most enlarged segment of the intumescencia cervicalis of twelve mammals and the relative average size of the largest nerve cell bodies found in the same localities. The diameters are taken within or exclusive of the pia mater spinalis and are from stained sections, the material having been dehydrated and embedded in celloidin and probably somewhat shrunken in consequence. The areas were determined by means of the EDINGER *projection apparatus* and the CORADI *planimeter*. The areas of outline tracings of projections of the sections enlarged 10 diameters were taken with the planimeter in terms of square millimeters. The results were then reduced by 100 to obtain the actual areas as given in the Table. The areas recorded in column 6 were taken in a similar way, but from separate outline tracings of the gray figure. In column 7 are given for each specimen the area of that portion of the gray figure the dorsal boundary of which runs parallel to and along the dorsal border of the commissura grisea. In this way that part of the substantia grisea which contains the larger cell bodies, is marked off. The differences therefore, between the areas in columns 6 and 7 represent the areas of the columnae posteriores. The average mean diameters of the cell-bodies (col. 1) were determined by measurement of the ten largest cells in three sections including and adjacent to that section whose dimensions and area are given. The two dimensions of each cell-body were measured, in each case, under a magnification of 712 diameters (ZEISS). The value of the spaces of the ocular micrometer were determined by means of a stage micrometer ruled into 1-100 mm. The method followed in judging a diameter involving the larger dendrites is shown in Plate XIII, where the lines crossing the cell body are the exact lines measured.

In the first place it is seen from Table III that while the dimensions of the medulla spinalis decrease gradually down the series, they are by no means constantly proportional to the size of the animal, nor do they vary with the variations in body weight. The adult elephant having a body weight of 8,000 pounds¹ is about six times as large as the average horse,² while

¹ The elephant from which the present specimen was obtained was estimated to weigh about 8,000 pounds. From measurements recorded by SCLATER ('79) and from information obtained through the kindness of the Zoological Society of Philadelphia, it appears that 8,000 pounds is a fair average for the Indian elephant. "Jumbo" reported to have been the largest elephant in captivity was not the heaviest. His great height (over 12 ft.) consisted in disproportionately long legs and a hump in his back. "Bolivar," the large Indian elephant now in the Philadelphia Zoo is probably actually the heaviest ever in captivity in America. His weight is now estimated at 12,000 pounds and he is 10 feet high. The African elephant is more slender than the Indian or Asiatic and probably does not weigh as much in the average. "Jumbo" was an African elephant. In a paper published in 1722, STUKELEY mentions having read of an elephant which had a height of 14 feet. He also notes that the African elephant is less in size than the Indian and is of a darker color.

² The horse dealers consulted place the average weight of the ordinary horse at 1,250 pounds. Rarely does even the draft horse acquire 1,800 pounds.

the mean diameter (col. 4) of its medulla spinalis, in the cervical region at least, is only about one and one third times as great as that of the horse. When compared with man, whose central nervous system is well developed in proportion to body weight, the elephant having a body weight fully fifty times that of man, has a medulla spinalis, the transverse dimensions of which, in the cervical region, are less than twice as great as those of man. Finally, when compared with the white mouse whose average body weight is about 20 grams, it will be found that the elephant is 180,000 times heavier than the mouse, while the mean diameter of its medulla spinalis is little more than 13 times as great, or ratio of 1:180,000 as compared with a ratio of 1:13.

These comparisons do little more than emphasize the generally accepted truth that the smaller the mammal, the greater is the proportional size of its central nervous system.

It is inadequate and unsatisfactory certainly to compare body weights with diameters of the medulla spinalis. The actual weights of the central nervous system or even of the medulla spinalis would of course give more satisfactory comparative relations, but unfortunately the weights of several of the specimens, especially the elephant, were not obtainable, and no records giving them have been found elsewhere. A knowledge of the third dimension would enable one to arrive at more expressive results, but the entire length of certain of the specimens (elephant, horse and ox) not having been obtained, comparisons involving this dimension are also impossible. However, it may be noted that if the shape of the body of the elephant is compared with that of the horse, man and the mouse, or in fact, with that of any of the other members of the series, the body of the elephant will appear proportionally short. KORSCH's observations (*loc. cit.*) give the medulla spinalis as terminating at the level of the 1st sacral vertebra. This is 10 segments before the exit from the canalis vertebralis of the last spinal nerve.

Since areas increase more rapidly than diameters, a comparison of the areas of the different transverse sections will give

results more nearly expressive of the relations sought. In column 5 of Table III the total areas are given of each of the transverse sections exclusive of the pia mater. To obtain these areas each section was first enlarged to reduce the error, and an outline tracing made of the projected image. The area of this tracing was then taken with the "Kugelrollplanimeter" (invented by G. CORADI) and the result divided by the square of the number of diameters by which the original had been enlarged. The planimeter used is recommended for its accuracy and enables one to obtain the area of a figure however irregular its outline. The machine automatically registers an amount from which the area of the figure can be computed to thousandths of a square mm. To insure no mistake and to minimize the possible error, each tracing was gone over with the planimeter three times. The areas recorded in columns 6 and 7 were obtained in a similar way.

Using the areas of the sections instead of their diameters in the comparisons, it will be found that the elephant having a body weight 6 times that of the horse has a medulla spinalis, the transverse section of which in the cervical region has an area but little more than 2 times that of the horse. Or, having a body weight at least 50 times that of man, the elephant has has an area of section only about 3 times of man. Conservatively speaking, the elephant is 180,000 times as heavy as the white mouse, but the area of the section of its cervical medulla spinalis is only 156 times that of the mouse. These results are somewhat higher than those obtained from comparing the diameters of the specimen.

If similar comparisons are applied to the other members of the series, results will be obtained gradually varying from the larger mammal to the smaller.

The general statement that the smaller the mammal the greater is its central nervous system in proportion to the size of the body, may be emphasized by making another comparison between the elephant and the mouse. If the size of the mouse is increased to the size of the elephant and at the same time the proportion maintained between the area of the section of

the medulla spinalis and the body weight of the mouse, a very interesting if not accurately illustrative result is obtained. Considering 20 grams or 1-23 of a pound to be average weight of the mouse and 8,000 pounds that of the elephant, then if a mouse of 1-23 of a pound has a medulla spinalis the area of whose section is 2.8 sq. mm., a mouse with a body weight of 8,000 would have a section with an area 23 times 2.8 times 8,000, or an area of 515,200 sq. mm. instead of 432.6 sq. mm. as possessed by an elephant of that weight. This number divided by 432.6 will give 1,191. In other words, a mouse as large as an elephant would have a medulla spinalis, a section of which in the cervical region would have an area 1,191 times that of an elephant. Further, in order to have an area of section 3 times that given by man, the elephant must have a body weight 50 times as great as man. In order to have an area of section only 3 times as great as that given by the mouse, the elephant must have a body weight of 155 pounds or 3,565 times that of the mouse.

The above seems to indicate that the medulla spinalis of the elephant must be more slender than that of the mouse and such comparison as is possible shows this to be the case. KORSCH records that his specimen, exclusive of the first two segments, had a length of 150 cm. In the *intumescentia cervicalis* this had a mean diameter of 25.5 mm. Measurements made of the corresponding portion of several mice show that exclusive of the first two segments the average length of the medulla spinalis is about 3.2 cm., while the average mean diameter of the largest segment of the *intumescentia cervicalis* is 1.7 mm. If the dimensions of the medulla spinalis of the elephant be reduced to a length of 3.2 cm. (that of the mouse) its mean diameter will then be only about 0.5 mm. instead of 1.7 mm. as possessed by the mouse.

A discussion of columns 6 and 7 is reserved for a subsequent paragraph. However, it may be here noted that the area of the *substantia grisea* varies in the main, with the area of the entire section, though the latter decreases more rapidly. The ox with a heavier body than the horse has both a smaller

area of entire section and a smaller area of substantia grisea in it. The areas of sections for the dog, monkey and cat are approximately the same, but the area of the substantia grisea in the sections is least for the largest of the three and greatest for the smallest. A glance at column 7 will show that the cat acquires its greatest area through the size of its columnae posteriores (substantia gelatinosa) and that, in reality, the monkey possesses the largest columnae anteriores and, as would follow, the greatest number of motor axones arising at this level. The elephant has an area of section 3 times as great as man and also an area of substantia grisea in the section 3 times great, while for the mouse, the area of the section from the elephant is 154 times that of the mouse, but the area of the contained substantia is only 54 times that of the mouse.

In column 1 of Table III are recorded the sizes of the cell-bodies situated in the columnae anteriores of the largest cervical segment of the different animals of the series. The size is expressed in terms of the average mean diameter of the ten largest cell bodies found in three adjacent sections, one of which being the section employed in obtaining the data given in the remaining columns of the Table. The measurements were made with an ocular micrometer and under a magnification of 712 diameters (ZEISS). In each case the two diameters measured were the longest diameter of the cell-body and the diameter at right angles to this. All diameters taken passed through the center involving the nucleus. When a measurement involved one of the larger dendrites, the diameter had to be judged by an approximate estimation of what the diameter would be were the section of the cell body a circular disc with the more visible portion of the dendrite included in it. A special effort was made to employ similar judgments in all cases. In order to avoid measuring the same cell body in two sections, and to assure the measurements passing approximately through the center, only such cell-bodies were measured as contained nucleoli. The method of measurements may be seen in Plate XIII where the shape and relative size is represented by one of the ten cell bodies measured from each of the specimens. The

lines shown crossing the cell-bodies are the identical diameters measured. The averages given in the Table were obtained by dividing by 10 the sum of the mean diameters of the ten cell bodies measured.

In Table III as well as in Plate XIII it can be seen that in passing from the elephant to the bat there is a general and fairly gradual decrease in the size of the cell body. This decrease however is very roughly and not at all directly proportional to the decrease in the size of the animals. The results give the dog as large a cell body as man, while the monkey has almost as large as the hog, and the difference between the rat and rabbit is equally as far from expressing the difference in the size of the two animals. Only the general statement may be made that the smaller mammals have the smaller cell-bodies in the columnae anteriores of the *intumescentia cervicalis*.

It will be noted that the bat seems to possess an appreciably larger cell-body than the mouse. This indicates a peculiarity of this animal shown by none other in the series. Sections from its *intumescentia cervicalis* revealed a lateral group composed of cell-bodies much larger than any others in the section. This group is the chief component of the *columna lateralis* of this animal. Their position leads one to assume that these large cell-bodies have to do with the innervation of the wings of the bat, a modification of the fore limbs not possessed by any other of the mammals in the series. Since the original plan called for measurement of the largest cell-bodies only, the measurements for the bat were made entirely from this group. The average would have been less than that for the mouse had the measurements been made from the much smaller cell-bodies occupying the other portions of the *columna anterior*.

In a few instances cell-bodies of neurones of animals varying in body weight have been measured by previous investigators. These show variations in size similar to those shown in Table III.

KAISER ('91) made some measurements of the cell bodies of the cervical region from a series of five mammals. His tissue was fixed exclusively in MÜLLER'S fluid, and his object be-

ing different from that here in mind, his measurements were not confined to any particular cervical segment. Among other points, he was concerned with the relation between the staining properties of the cell body and its size. He describes the larger cell bodies as "Chromophobic" as compared with the smaller or "Chromophilic." We are concerned here only with larger or chromophobic group. KAISER records only the mean diameters of the largest and smallest (the extremes) of this group rather than averages as here desired. His results for these may be tabulated as follows:

Animal	CHROMOPHOBIC CELL BODIES mean diameters in micra.	
	smallest	largest
Man (<i>Homo</i>)	23	59
Monkey (<i>Cercopithecus sinicus</i>)	33	60
Rabbit (<i>Cuniculus domesticus</i>)	41	60
Mole (<i>Talpa europaea</i>)	36	54
Bat (<i>Plecotus auritus</i>)	28	53

Since KAISER gives extremes of a group rather than averages and does not confine his search for such within any given segment, his measurements of the largest cell-bodies can not be compared with those of Table III. His largest cell for man with a mean diameter of 59 micra compares favorably with the average mean diameter of 58 micra recorded in Table III. His monkey, *Cercopithecus sinicus*, is a smaller species than *Cynocephalus babuin* (Arabian baboon) and yet the largest cell body found by KAISER for this specimen is appreciably larger than the average of the ten largest found for the baboon. The bat, *Plecotus auritus* is also larger than the small *Atalapha cinerea* and KAISER finds that it has larger cell-bodies in its cervical medulla spinalis. KAISER finds a larger cell body for the white rabbit than any found by the author. This is difficult to explain. It may be that certain of the cervical segments which KAISER examined may contain larger cell bodies than the one segment to which the author was confined. It is known that

throughout the extent of the medulla spinalis, the cell-bodies, within certain limits, vary in size for the different localities—those of the thoracic region having an average diameter less than those of either the cervical or lumbar. KAISER's results must differ from the author's chiefly from the fact that looking for extremes he employed a much larger number of cell bodies from which to choose his largest.

WALDEYER ('89) measured a small number of cell bodies of the IIIrd and IVth cervical segments of a two year old male gorilla, and from his records an average mean diameter of only 32 micra is obtained. His measurements deal with the ventral group of the columna anterior and, unless the gorilla differs from the mammals with which the author is acquainted, this group does not contain the largest cell bodies at this level. They should be found in one of the lateral groups but, even for the ventral group, without knowing anything of the peculiarities of the gorilla in this respect, one would say that an average of 32 micra is small for an animal of this size. The two year old gorilla in all probability has cell bodies smaller than the adult but only slightly so. So far as has been investigated, animals of the same species have in early life smaller cell-bodies of neurones than the adult. In the neurological laboratory with which the author has been connected this has been repeatedly proven for the white rat, and KAISER ('91) in another series of measurements has proven it true for man and the white rabbit.

CAVAZZANI ('97) determined the average mean diameters of the cell-bodies found in the ganglia spinalia of a series of mammals to which he also added the frog. His material was fixed either with osmic acid or MÜLLER's fluid and, in some cases, his measurements were made from teased preparations instead of from sections. His averages in each case are based upon a large number of measurements (200-500) and should therefore mean more for the ganglia than averages of a small number of cell bodies especially chosen for their large size. His measurements are made from the ganglia of the cervical, thoracic and lumbar regions but are not confined to a given segment of

either of the three regions. The species of his monkey and rabbit are not given. His results may be arranged as follows :

<i>Animal</i>	AVERAGE MEAN DIAMETERS OF CELL BODIES OF GANGLIA SPINALIA IN MICRA.		
	<i>Cervical</i>	<i>Thoracic</i>	<i>Lumbar</i>
Ox (adult)	107	105	107
Man (30 years)	74	55	72
Dog (adult average of bull, shepherd and fox-hound)	75	64	74
Cat (adult)	80	67	80
Monkey (2,000 grams)	52	44	55
Rabbit (adult)	53	51	52
Hedge-hog (young-125 grams)	76	65	73
White rat (adult)	34	29	
Frog	55 (IIInd)		65 (VIIIth)

BÜHLER ('98) also made some measurements from the ganglia spinalia of a series of vertebrates. His series involved man, dog, cat, rabbit, pigeon, frog, lizard, and white fish. He did not arrange his results according to the segments from which they were obtained. However, as to general size his results pertaining to mammals agree with those of CAVAZZANI.

Upon the measurements of CAVAZZANI and BÜHLER the following statements may be made with reference to the ganglia spinalia :

1. That the size of the cell-bodies of the ganglia spinalia varies in the different regions of the medulla spinalis of the same mammal.

2. That the size of the cell-bodies of the ganglia spinalia varies in the same regions of the medulla spinalis of different mammals.

3. That these variations in the size of the cell-bodies are not directly proportional to the variations in the size of the body of the animal, though in general the larger mammal possesses the larger cell-bodies in its ganglia spinalia.

From what we know of the sizes of the cells of the other tissue systems of the different mammals, one can scarcely expect a variation in the size of the cells of the nervous system in marked proportion to the variations in body weight. While it may be claimed that there is a slight proportional variation in the size of the tissue cells among the mammals, such a claim would be wholly untenable were the whole of the *Vertebrata* included. Both CAVAZZANI's and BÜHLER's measurements for the frog show it to possess a nerve cell body larger in proportion to its body weight than is possessed by any of the mammals. And it is further well known that most of the tissue elements of the still lower and small vertebrates are larger even than the corresponding tissue elements of the higher vertebrates.

But it must be remembered that with reference to the neurone, the size of the cell-body is but a feeble expression of the real size of the neurone. The difference brought out in the above tables can be little more than indicative. The neurone is a peculiarly differentiated tissue element in which the far greater part of the cell substance is sent out in more or less far reaching processes. DÖNALDSON ('98) has made computations showing the relation between the volume of the cell-body of certain of the neurones of the central nervous system of man and the volume of its longest process, the axone, and has found that the axone may have a volume 187 times that of the cell-body from which it is an outgrowth. This computation of course does not include the medullary sheath of the axone which must be considered as an acquired structure. One must remember therefore that the elephant, while having in its *intumescentia cervicalis* a cell-body appreciably larger than any of the other mammals investigated, must have an entire neurone whose total volume exceeds that of the other mammals to a far greater extent than is indicated by the mere diameter of the cell body.

The majority of the large cell bodies (those measured) of the *intumescentia cervicalis* are situated in the *columna lateralis* (lateral horn). These innervate (KAISER ('91) COLLINS ('94) SANO ('97)) the muscles of the fore leg. An axone, then,

passing from the medulla spinalis to the fore foot of the elephant would have a length at least 7 feet¹ or 2128 mm. Assuming that the larger cell-bodies give origin to the larger axones (DONALDSON ('98)) and that some of the larger axones extend to the fore foot, measurements were made of the diameter exclusive of the medullary sheath of a number of the larger axones of the radix anterior of the elephant which were cut transversely and mounted in company with the sections containing the cell bodies measured. These axones were suited to the purpose not only because they belonged to the radix anterior of the same segment as the cell-bodies concerned, but because they had been subjected to the identical conditions in dehydration, embedding, etc. applied to the cell-bodies. The average diameter of these axones (axial spaces within sheath) proved to be 11.76 micra. This gives the section of the axone an area of 108.55 sq. micra. Considering the axone as a cylinder having this as the area of its base and an altitude of 7 feet, such a cylinder has a volume of 230,994,400 cu. micra. Then if the cell body be considered as a sphere with a diameter of 84.4 micra, such a sphere has a volume of 314,634 cu. micra. In other words the axone arising in the intumescentia cervicalis of the elephant may have a volume 734 times the volume of the cell body giving origin to it. And the volume of the entire neurone, exclusive of collateral branches and the greater portion of the dendritic processes, may be 231,309,034 cu. micra.

For man the average caliber of the axone (axial space) of the radix anterior cut transversely in company with the sections containing the cell bodies measured, was 8.4 micra. This gives the section of the axone an area of 55.4 sq. micra. 800 mm. is considered a conservative estimate of the average length between the intumescentia cervicalis of man and the muscles

¹ An elephant of 8,000 pounds has a height of fully 8 feet from sole of foot to top of back between shoulders. Twelve inches of this is allowed for the thickness of the tissue overlying the medulla spinalis. This height for "Bolivar" is about 10 feet and records obtained through the kindness of WARD'S Natural History establishment show that the corresponding height of "Jumbo" was 12 feet. Jumbo's greatest height was produced by an extraordinary arch in the back.

of the fingers. Then the axone extending this distance has a volume of 44,312,000 cu. micra or 434 times the volume of the cell body giving origin to it. Adding 102,109 cu. micra (the volume of the cell body with a diameter of 58 micra) to the volume of the axone, gives the entire neurone a volume of 44,414,109 cu. micra. By the necessary divisions it will be found that the motor neurone of the cervical region of the elephant may be 5.2 times that of man, while the diameter of the corresponding cell-bodies is only 1.3 times that of man. The volume of the cell body of the elephant, the area of the corresponding section of the medulla spinalis of the elephant, and the area of the section of the substantia grisea are, all three, about 3 times as great as in man though the body weight of the elephant is 50 times as great as man's. These coincident ratios between the elephant and man seem, however, to be exceptional for the series.

For the mouse the corresponding cell-body having a mean diameter of 27.4 micra (Table III) would have a volume of 7974 cu. micra. Measurements of the corresponding axones of the radix anterior give them an average diameter of 4.2 micra, and thus an area in section of 13.9 sq. micra. Measurements of eight adult mice give 35 mm. as the conservative average distance between the medulla spinalis and the center of the fore foot. An axone extending this distance would therefore have a volume of 486,500 cu. micra, or 61 times that of the cell body from which it arises. The volume of the axone added to the volume of the cell-body gives 494,474 cu. micra as the volume of the entire neurone.

Comparing these quantities for the mouse with the corresponding quantities for the elephant, it is found that the entire neurone arising in the *intumescentia cervicalis* of the elephant may be 469 times as voluminous as that of the mouse, while the volume of corresponding cell-body is 39 times as great, and the mean diameter of the cell-body only about 3 times as great as that of the mouse. It has already been shown that the area of the section of the medulla spinalis of the elephant is 154 times the area of the corresponding section of the mouse, while

the area of the substantia grisea contained in the section of the elephant is 54 times that of the mouse and its body weight 180,000 times greater.

Comparing man with the mouse, man has a neurone whose entire volume is 90 times greater than that of the mouse; a cell-body whose volume is 13 times greater; the mean diameter of the cell body, 2 times greater; a section of medulla spinalis with an area 47 times that of the mouse; an area of substantia grisea in section 15 times as great, and a body weight 3628 times as great.

The above comparisons indicate that in a series of mammals of varying body weights, the volume of the entire neurone varies more nearly in proportion to the variations in body weight than either the area of the section of the medulla spinalis, the area of the substantia grisea contained in the section, or either the diameter or volume of the cell-body contained in the substantia grisea.

The other members of the series would show slightly different and equally interesting relationships but it would be too tedious to continue these comparisons further. The elephant, man and mouse are chosen because they represent species having fairly uniform size, because they are forms of which we have a more definite impression, and because at the same time they represent the extremes and the mean of the series.

From the measurements cited and those recorded in Table III, and from the above deduced comparisons, it may be advanced:

1. That the size of the large cell bodies situated in the columnae anteriores as well as that of the cell-bodies in the ganglia spinalia varies appreciably in adult mammals of different sizes.
2. That in general the larger mammals have the larger cell-bodies in both localities, but that in either the variations in the size of these cell-bodies do not occur in the same ratios as the variations in the size of the body of the animals, the cell bodies varying in much smaller ratios than the body weights.
3. That the variations in the volumes of the cell bodies do not occur in higher ratios than the variations in the areas of

the transverse sections of the medulla spinalis, and in no higher ratios than the variations in the areas of the substantia grisea contained in the sections.

4. That in the larger mammals especially, but a small fraction of the entire neurone is represented in the cell-body or the ordinarily visible portion of the neurone.

5. That the variations in volume of the entire neurone occur in higher ratios and are therefore more nearly in proportion to the variations in body weight than either the volumes of the cell-bodies, the areas of the transverse sections of the medulla spinalis, or the areas of the substantia grisea in the sections.

Some interesting relations may be seen by comparing the areas of the substantia grisea and the substantia alba in the transverse sections from the different members of the series, and also by comparing the area of the section of the cell body with the area of the section of the substantia grisea containing it. The data for these comparisons are contained in Table III, but that the comparisons may be more easily made and the relations more readily seen, the necessary computations are made and tabulated as follows:

TABLE IV.

Animal. Arranged according to normal body weight.	(1) Area of substantia gri- sea (total gray figure) in section. sq. mm.	(2) Ratio of area of sub- stantia grisea to area of entire section.	(3) Area of substantia alba in section. sq. mm.	(4) Ratio of area of substan- tia grisea to area of substantia alba.	(5) Area of section of aver- age largest cell-body. sq. mm.	(6) Area of substantia gri- sea ventral to dorsal bor- der of commissura gri- sea. sq. mm.	(7) Ratio of area of average cell-body in section to area of substantia grisea as in column 6.
Elephant	76.5	5.7	356.2	4.7	.0056	52.9	9442
Ox	29.7	6.9	178.1	5.9	.0033	20.5	6195
Horse	34.3	6.2	177.1	5.2	.0029	22.3	7703
Man	21.8	6.1	110.5	5.1	.0026	15.6	6002
Hog	14.1	5.9	69.8	4.9	.0024	7.9	3283
Dog	8.9	3.3	20.5	2.3	.0027	5.7	2119
Monkey	9.2	3.2	20.1	2.2	.0023	6.2	2691
Cat	10.5	2.8	19.0	1.8	.0022	4.5	2021
Rabbit	4.1	3.8	11.2	2.8	.0012	2.7	2229
Rat	2.4	2.5	3.6	1.5	.0009	1.3	1489
Mouse	1.4	2.1	1.4	1.0	.0006	.8	1375
Bat	0.9	1.8	0.8	0.8	.0007	0.7	928

TABLE IV. Given for comparison of the actual and relative areas of the substantia grisea, the substantia alba, and the areas of the sections of the cell-bodies as found in the transverse sections of the largest segment of the intumescencia cervicalis of the animals named. The areas of substantia grisea recorded in columns 1 and 6 are brought forward from Table III, under which the method of obtaining the areas is described. The area of the substantia alba (column 3) is obtained in each case by subtracting the area of substantia grisea from the area of the entire section (column 5, Table III). The area of the section of the cell-body (column 5) is obtained for each entry by considering the cell-body as a circle with a radius of one half the average mean diameter of the cell-body as recorded in column 1 of Table III, and reducing the result obtained to terms of sq. mm. The ratios given in columns 2, 4, and 7 are obtained for each specimen by the division of the first factor mentioned in the heading of the column into the second, and thus represent the relative amounts of the two factors. For example, in column 2, for the elephant the ratio of the area of substantia grisea (column 1) is to the area of the entire section (column 5, Table III) as $\frac{432.6}{76.5}$ or as 1 is to 5.6. In other words, the area of the entire section is 5.6 times the area of the substantia grisea contained in it.

All particulars found in material from a single individual may not be common to the class. Certain of the details given in Table IV might have been materially altered had a number of individuals been investigated in each case instead of one and the records in the Table computed from averages from different individuals. Since this would have been an extremely laborious task, certain assumptions must be allowed.

Assuming, then, that what is true for the individual is true for the class, attention is called to the columns of Table IV as giving reasons for the following statements:

1. The area of the substantia grisea (col. 1) in the transverse section of the intumescencia cervicalis decreases gradually with the decrease of the size of the animal, and the ratios of the area of substantia grisea in section to the area of the entire section are similar for animals approaching each other in size of body.

The decrease is not a regular one. The ox, with a greater average body weight than the horse and a larger cell-body at this level, gives a section both whose entire area and the area of whose substantia grisea is less than that of the horse. The former deficiency on the part of the ox is shown in columns 2 and 3 to be entirely due to the smaller amount of substantia grisea, for the area

of substantia alba in the section is even greater than that of the horse. The monkey (Arabian baboon) was appreciably larger than the cat, and the dog was larger than either, yet the three give sections of medulla spinalis the entire areas of which (col. 5, Table III) are about the same. Notwithstanding the approximate equality of the three as to the area of entire section, the monkey exceeds the dog in the area of substantia grisea in section, and the cat, the smallest of the three, exceeds both the monkey and the dog in this respect. The area of the entire section of the elephant is 3.3 times that of man and the area of its substantia grisea is 3.5 times as great as man's. In other words, the area of the entire section of the elephant, in round numbers, is to the area of the entire section of man as the area of the substantia grisea of the elephant is to the area of substantia grisea of man. Similar proportions exist between the elephant and the ox, the horse, hog and dog. The proportion is destroyed in the monkey and cat, the area of the entire section of the elephant being 15 times greater while the area of the gray substance is roughly only 8 times as great. For the remaining members of the series, the relations are different in each case, the relative area of the substantia grisea being greater in the smaller animals. The above comparisons seem to indicate that the relation between the bulk of the medulla spinalis and the amount of its substantia grisea is more nearly constant for the larger mammals than for the smaller.

These relations are perhaps but another expression for what is shown in columns 2 and 4 of Table IV. In column 2 the ratios between the area of the entire section and the area of the substantia grisea contained in it are given for each specimen and thus may be compared among themselves instead of each being compared with the conditions found in one individual, as above. It will be seen that these ratios allow the members of the series to be roughly divided into three groups: For the elephant, ox, horse, man, and hog, the area of the entire section is approximately 6 times the area of the substantia grisea contained in it; for the dog, monkey, cat, and rabbit, it is about 3 times that of the substantia grisea, and for the rat,

mouse and bat, about 2 times that of the substantia grisea. By comparing columns 3 and 4 it will be seen that column 2 is but another form of the ratios given in column 4, and that therefore the above statement will apply also to the ratios between the areas of substantia grisea and the areas of substantia alba contained in the sections.

It is evident, then, that animals approaching each other in size of body have similar ratios between the area of substantia grisea and the area of medullated axones in transverse sections of the intumescencia cervicalis. In the elephant, however, much the largest animal in the first group, the area of medullated axones exceeds the area of substantia grisea to a less extent than in any other of this group.

2. The area of the substantia alba in the different sections (column 3) decreases more regularly and more rapidly than the area of the corresponding substantia grisea, and in the larger specimens, the area of substantia grisea is exceeded to a greater extent by the area of the substantia alba surrounding it than is the lesser area of substantia grisea in the smaller specimens.

Reading columns 1, 2, and 3 upward, it will be seen that as the specimens increase in size the increase is due more to the increase in the area of the medullated axones than to the increase in substantia grisea. The cell bodies contained in the substantia grisea give origin to a large proportion of the medullated axones going to form the substantia alba (long and short association and commissural pathways). A greater amount of substantia grisea is coincident with a greater number of cell-bodies situated in it. This greater number of cell-bodies must be coexistent with the presence of a greater number of medullated axones in the section: axones arising (1) in other levels and coursing in the section to connect with the cell-bodies in the vicinity of the section, and (2) axones arising from the cell-bodies themselves and passing to other levels of the medulla spinalis or to the peripheral system. It has been shown that the axone of the neurone even exclusive of the medullary sheath may be many times the volume of the cell body giving

origin to it. Therefore what is shown in columns 1 and 3 is to be expected, namely, that an increase in substantia grisea is accompanied by a more rapid increase in substantia alba. Column 4, giving the ratios of the two substances, shows that for the larger specimens the area of the substantia alba is approximately 5 times as great as that of the substantia grisea, while for the smaller specimens it is 2 or less times as great.

3. In the series of specimens the ratio of the area of the section of the cell-body to the area of the substantia grisea containing it decreases with considerable regularity from the largest to the smallest specimen, but the decrease is not in proportion to the variations in the areas of the sections of the cell-bodies.

These comparisons may be made in columns 7 and 5. Column 5 is derived from Table III and contains for each specimen the area of the section of the average large cell-body computed from the mean diameters recorded there. Thus the areas of the cell-bodies differ among themselves much as the diameters from which they are derived. For a comparison of the area of the section of the cell-body with that of the substantia grisea, it was thought better to use only the area of that part of the substantia grisea which contains the cell-bodies employed. The amount of substantia grisea in the columnae posteriores depends largely upon the amount of substantia gelatinosa present. This latter varies greatly in relative amount in the different individuals as well as in different levels of the same individual and has necessarily nothing to do with either the size or the number of the cell-bodies in the columnae anteriores. Then to obtain what are considered the more expressive ratios, the areas of the columnae posteriores were excluded. In column 6 are recorded in each case the area of that part of the gray figure ventral to a line drawn through the gray figure along the dorsal border of the commissura grisea. The ratios in column 7 are obtained by dividing in each case the area of this portion of the substantia grisea by the area of the section of the average large cell-body (column 5) and thus express the number of times

the area of substantia grisea is greater than that of the section of the cell-body.

In the elephant the area of the substantia grisea is 9,000 times that of the cell-body, while in the bat it is only 900 times as great, the ratio decreasing through the series with tolerable regularity.

The greater amount of substantia grisea contains not only the larger cell-bodies, but also the greater number of cell-bodies. Therefore the ratios between the areas of the section of the two do not decrease as the areas of the sections of the cell bodies do, and therefore decreasing rather than constant ratios result.

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EXPLANATION OF THE ILLUSTRATIONS.

PLATE IX.

Fig. 1. Outline sketch of the dorsal aspect of the portion described of the medulla spinalis of the elephant. The slanting cephalic end shows the plane of the knife, in the foramen magnum, severing the specimen from the encephalon. The specimen was divided for fixation and the sketch is made from the subjoined pieces. Roman numerals in sketch indicate segments. Transverse lines, the levels from which sections were taken for the illustrations as indicated. *F. r.*, Fila radicularia of radix posterior; *C. s.*, calamus scriptorius. $\times \frac{1}{3}$.

PLATE X.

Fig. 2. Photograph of transverse section through calamus scriptorius and caudal extremity of oliva inferior. $\times 3$.

Fig. 3. Companion to *Fig. 2.* *C. a. p.*, commissura alba posterior; *D. l.*, Decussatio lemniscorum; *N. f. c.*, Nucleus fasciculi cuneati; *N. f. g.*, Nucleus

fasciculi gracilis; *N. n. h.*, Nucleus nervi hypoglossi; *O. a. m.*, Nucleus olivaris accessorius medialis; *O. i.*, Nucleus olivaris inferior; *P.*, pyramids; *S. g. R.*, Substantia gelatinosa Rolandi.

PLATE XI.

Fig. 4. Transverse section through decussatio pyramidum and caudal portion of nucleus fasciculi gracilis. Photograph. $\times 3$.

Fig. 5. Companion to Fig. 4. *D. p.*, decussatio pyramidum; *F. c. i.*, fasciculus cerebro-spinalis internus; Other references same as in Fig. 3. Slightly diagrammatic as to decussating pyramidal axones.

Fig. 6. Detail from Fig. 4. Involving the region between the columnae anteriores and showing the general course of the decussating pyramidal axones as they pass from the pyramid below to collect in the fasciculus cerebro-spinalis internus above. The magnification is not great enough to show the axones themselves but their beginning course is indicated by the arrangement of the connective tissue trabeculae. The open spaces are blood vessels. $\times 10$.

Fig. 7. Transverse section through VIth cervical segment of the medulla spinalis. Photograph. The dark bodies in the lower left of the figure are fila radicularia of the radix anterior which by accident were folded under in mounting the celloidin section. Other such fila are vignettted out of the print. $\times 3$.

Fig. 8. Companion to Fig. 7. *A. s. a.*, arteria spinalis anterior; *C. a. a.*, commissura alba anterior; *F. c. i.*, fasciculus cerebro-spinalis internus; *F. g.*, fasciculus gracilis; *R. p.*, radix posterior. The position of the canalis centralis is shown.

PLATE XII.

Fig. 9. Detail from Fig. 7, showing the fasciculi cerebro-spinales interni as they are situated in the commissura grisea between the dorsal portion containing the canalis centralis and the commissura alba posterior, and the ventral or commissura alba anterior. Numerous blood vessels are shown. $\times 10$.

Fig. 10. Detail from transverse section through the IVth Thoracic segment. On same scale as Fig. 9. Shows appearance and decrease in size of fasciculi cerebro-spinales interni and the size and appearance of the nucleus dorsalis at this level. The angle of the columnae posteriores may be noted, and on the lower left of the figure the thickness of the columna anterior. $\times 10$.

Fig. 11. Photograph of transverse sections from VIIIth Thoracic segment. Showing the proportional amount of substantia grisea at this level, the general shape of the gray figure, columnae posteriores and anteriores, the appearance of the fasciculi cerebro-spinales interni, the nuclei dorsales, the relative thickness of the dura mater spinalis, etc. $\times 3$.

Fig. 12. Companion to Fig. 11. *N. d. (C. c.)*, nucleus dorsalis (CLARKE'S column); Other references same as in Fig. 8. *F. g.* and *F. c. i.*, much less than in cervical VI (Fig. 8).

Fig. 13. Detail from Fig. 11. Given to compare appearances of the fasciculi cerebro-spinales interni, nuclei dorsales, columnae anteriores and commissura grisea with appearance of these structures as given on same scale in Figs. 9, 10, 14, and 15. $\times 10$.

Fig. 14. Photograph of central region of transverse section through

caudal end of Thoracic II. Shows beginning of the comparatively sudden departure of axones from nucleus dorsalis. Nucleus on right of figure shows axones leaving nucleus and crossing cervix of columna posterior to enter funiculi laterales. In nucleus on left this process has not yet begun. Shows appearance of nucleus in double contour as it occurs in this segment and in segment caudad to this. *F. c. i.*, larger than in Fig. 10 (Thoracic IV). $\times 10$.

Fig. 15. Photograph of one side of central region of section through Thoracic II, about 1 cm. cephalad to Fig. 14. Showing the level at which the departure of axones from the nucleus dorsalis is at its maximum. In leaving the nucleus, axones pass obliquely cephalad and thus their entire course is not shown in transverse section. *F. c. i.*, nearly as large as in cervical VI (Fig. 7). Commissura alba anterior involves pia mater of fissura mediana anterior. $\times 10$.

Fig. 16. Slightly diagrammatic reconstruction giving summation of appearances as seen in sections between those represented in Fig. 14 and Fig. 15. *A*, afferent axones (from radix posterior and fasciculus cuneatus) coursing toward and into nucleus dorsalis, *Nd.* *D.*, small longitudinal fasciculi of afferent axones (*A*). *C*, axones from nucleus dorsalis crossing cervix columnae posterioris to enter funiculi laterales, probably fasciculus cerebello-spinalis.

PLATE XIII.

The purpose of the twelve figures of this plate is to show the comparative size and the shape in section of the large cell-bodies present in the columnae anteriores in the thickest segment of the intumescencia cervicalis of the different mammals named. They are arranged in the order of the normal body-weight of the animals. Each figure represents one of the ten largest cell-bodies found in three adjacent sections of the segment and which were measured to obtain the average mean diameters recorded in column 1 of TABLE III. Under each figure is given the actual diameters of the cell-body in terms of micra and the name of the animal from which it was taken. The lines drawn through each figure represent the diameters which were measured and also show the method employed in judging the diameters which involved the larger dendrites. All the figures are camera drawings made under a magnification of 712 diameters. They are reduced to scale. ZEISS apparatus was used throughout for both the measurements and the drawings.

OBSERVATIONS ON THE POST-MORTEM ABSORPTION OF WATER BY THE SPINAL CORD OF THE FROG (*RANA VIRESCE*NS).

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In some previous investigations on the weight of the spinal cord of the frog (1, 2), it was found that if the cord were left in a frog for 24 hours or so after death, it had a weight much greater than that of the cord removed from a frog of the same size, immediately after it had been killed. It was assumed at the time that this post-mortem increase in weight was due to the absorption of water. To test this assumption and to obtain more extended data on this reaction, the present investigation was undertaken.

Introduction.

In studying the absorption of water by the spinal cord of the frog after death, we have had in view the collection of information which would serve to control errors which might arise when determining the weight and size of the spinal cord in this animal, and also be of use in interpreting the histological pictures to be obtained from the spinal cords taken from frogs at different periods after death. In the course of this work we have found several interesting sources of error.

On collating our various observations previous to this investigation, we are impressed by the fact that the living frog in this region is an animal continually changing from month to month, utilizing the brief period between April and October, first for reproduction, next for growth and active feeding, and finally, for a somewhat prolonged preparation for its final disappearance in the mud during the winter sleep.

In this series of changes between the appearance of the frog in the spring and his disappearance in the autumn, the reaction of the entire frog towards water appears to undergo a peculiar though regular alteration. In general, we get the impression that the frog contains a larger amount of water during the spring and early summer, and that this amount decreases gradually up to the time of hibernation, during which time the amount of water is at a minimum. As we have shown elsewhere (1, 2), the water taken up by the frog can be entirely absorbed through the skin alone, and in the absence of any direct observations showing that the water is taken by the mouth, we may conclude that the skin is practically the only channel by which the water passes into and out of the tissues.

What the conditions are which determine when the living frog shall take up more water and how much shall be absorbed, it was not our purpose to determine. Though it appears very probable that the power of nervous system at least to absorb water under the conditions offered by these experiments varies with the season. We wish here merely to insist on the normal existence of a rhythmic variation in the amount of water and on the fact that this variation affects the weight of the spinal cord. Our attention was turned to the normal variation in the weight of the nervous system and its percentage of water, by the fact that the present series of observations were made mainly in the latter portion of the summer of 1900. When the weights of the fresh spinal cord of this present series were compared with those which had been taken a year previous (2) and which were in a large measure obtained during May and June (though some of the observations were made later), we found the curious fact that the earlier records gave higher weights, the frogs compared being of the same body-weights and lengths. On comparing the few observations which had been made during the same months in the two series, we found that the cord weights under these conditions were very similar. On examining the earlier paper just alluded to, for cases where frogs of the same weight had been dissected both in the spring and in the autumn, we found that within this series the spring frogs

yielded the higher weight of the cord. It appears therefore, that in the two independent series of observations, made by similar methods but by different persons, the frogs dissected during the same months were alike in the weights of their spinal cords, while those dissected during different months differed. If, then, season is one determining factor, we can see without entering upon the details that frogs of a given weight or of a given length, have in the spring and summer heavier spinal cords than in the autumn, the difference in favor of the former group being sometimes as great as 25 %.

The cause of this excessive weight of the spinal cord in the spring frogs is still to be investigated, although one thinks of course, of an excess of water as in the main responsible for it; but that can only be determined by further investigation. Pursuing the usual methods of work, this investigation has extended over several months, but we have only recently appreciated that by thus extending it, we were working in the different months from midsummer to autumn, with frogs normally dissimilar in the absolute weight of their spinal cords and in their powers of absorbing water, and hence giving us results which probably show a smaller range than would have been found if all the frogs had been examined during the season when they were capable of the maximum absorption.

The use to be made here of the relations just described is as a basis for comment on the records about to be given so that they may be more fairly compared.

What has been said should be understood to apply strictly only to the species of frog which we have used. It probably applies in some degree to other species also, but thus far only casual experiments on the bull-frog (*Rana catesbiana*) have been made. It is possible of course, that other species, more fixed in their habits i. e., not wandering so far from standing water, may possess a different curve representing their cord weight and its powers of absorption, but it seems probable that all frogs in this neighborhood pass through a similar seasonal change. From this it follows, of course, that in undertaking investigations like the one here described, only frogs of the

same species should be used for comparative results, and that particular attention should be paid to the season of the year at which the observations are made. Moreover, to give reliable results, we have found that the frogs must be free from wounds for the frog in which abrasions of the skin on the feet or nose have been present for some time, react very differently from the normal frog, the spinal cord after death rapidly absorbing water to a large amount, and becoming very soft.

Moreover, many of the frogs of the species which we employed are infected with parasites (*Distoma*). These sometimes accumulate in the pia of the spinal cord, and may be present there in sufficient quantity to materially affect its weight. The cord therefore, should be examined for the presence of such parasites, an examination which may be carried on under a hand lens. In addition, there is always the normal variability of the individual in weight and length of the body, and the development of the nervous system, so that for satisfactory results, we can hardly rely on individual observations, but must use a method of averages.

As far as the spinal cord is concerned, the principal variation which occurs in the frogs of the sizes here used is in their length, and this usually modifies their weight. In order, therefore, to get rid of the individual variability in the length of the cord, we have in all cases, divided the total weight of the cord in grams, by its length in millimeters, and thus obtained the weight of an average millimeter of cord, the whole mass of the cord being conceived of as forming a regular geometrical figure, the length of which was equal to the observed length of the cord.

The weight of the "standard millimeter of cord" thus obtained, gave us the numbers which have been used for comparison.

Manner of Preparation.

To obtain the data used in the tables given farther on, the preparation of the frog was conducted as follows: Recently caught specimens of *R. virescens* were employed. Two

specimens similar in body weight and length were selected and killed with chloroform. After death each was examined alone in the following manner: It was weighed in a closed box to a centigram; the weight of the ovaries when containing developed ova, being deducted from the body weight. The contents of the stomach were also removed when necessary. The length of the vertical line from the tip of the nose to the tip of the longest toe was taken in millimeters—the frog being suspended from its lip. From this point on, the treatment of the two frogs was different. The first frog, in future to be spoken of as the “control frog,” was at once eviscerated. The spinal cord was exposed; the length of the cord between the tip of the calamus scriptorius and the origin of the dorsal roots of the Xth (last) spinal nerve was determined under a dissecting microscope; then the cord was removed between these limits, the nerve roots being cut away at their superficial origin. The cord was put in a closed weighing bottle, examined for parasites with a hand lens, and if normal, weighed to the tenth of a milligram. Immediately after the determination of the body-weight the second frog, in future to be known as the “absorbing frog,” was put belly down at the bottom of a litre glass jar. There it rested on a layer of shot which had been put in the jar to sink to within a couple of centimeters of the surface of the water in which the jar floated. The surrounding water was held in a large aquarium and kept constantly flowing, so that the temperature within the jar containing the frog was very close to that of the tap water flowing through the aquarium. The jar was closed at the top by dense wire gauze, through which a thermometer was inserted, the bulb being at the level of the frog. There is of course some evaporation and hence loss in weight in the absorbing frog. This has been determined under the conditions here used to be less than 4% of the body weight and the error due to it has been neglected. So far as it goes, it tends to diminish the gain in weight exhibited by the cord of the absorbing frog. At the end of the time chosen, the “absorbing frog” was taken from the jar and the cord removed, measured and weighed, according to the method used for the

control frog. When the solids and water in the cord were to be determined, the cords were dried at about 85°C ., complete drying being accomplished in about 24 hours. In making a comparison of the results, the average weight of "the standard millimeter of cord" was the datum used in each case.

In presenting our results, we shall give averages together with the records for the limiting cases, but the series of individual observations is omitted. The various tables have been constructed in the following way. There are given first the date of observation, then the limits of the room temperature and of the jar containing the absorbing frog. Finally, a statement of the general conditions to which the absorbing frog was subjected. Beyond this it will be probably most advantageous to explain Table I in some detail, and then comment on the subsequent tables in so far as they depart from the form there used.

Experimental Results.

In the first instance we sought to determine the increase in weight of the absorbing cord under ordinary laboratory conditions. Table I is based on the comparison of eleven pairs of frogs. In the Table they are presented in three groups, being divided according to body weight. The observations were made between July 20th, and July 30th, on frogs caught within three days and kept in a dark tank through which tap water was constantly flowing. There were elevations in the tank so that the frogs could be in or out of the water at will.

Within in the jar containing the absorbing frog the temperature ranged from 20° - 22°C . The absorbing frog was not dissected until 24 hours after death.

TABLE I.

	Body Weight in grams.		Percentage gain in "Standard millimeter" of the spinal cord of the absorbing frogs.	
	Extremes	Average	Average	Extremes
Group I				
4 pairs	(16-18.1)	17.1	13.5	(5.3-17.8)
Group II				
4 pairs	(23.4-30.7)	27.5	15.1	(6.1-30.7)
Group III				
3 pairs	(33-50.3)	41.8	25.1	(16.9-36.3)

To explain Table I we need to analyze the record in the first line only (Group I), as the construction of the other lines is quite similar to it.

Group I consists of 4 pairs of frogs—a pair being always killed at one time and one frog dissected at once, while the other was put aside; in this case for 24 hours. In the first column under body-weight in grams—*extremes*—is given the weight of the lightest (16 grams) and the heaviest (18.1 grms). The average of the entire group of 8, appears in the next column as 17.1 grams. From each of the four “control” frogs, the spinal cord was removed between the limits previously noted and the length of the cord measured to tenths of a millimeter. Taking now the sums of the weights of all the cords and the sum of their lengths, we divide the former by the latter and obtain the average weight for one standard millimeter of cord. The same operation is repeated in the case of the spinal cords of the “absorbing frogs” which had been allowed to lie for 24 hours in the nearly closed vessel as above described. On comparing each of the pairs for differences in the weight of the standard millimeter, it was found, as shown in the last column, that in one pair the absorbing frog had gained only 5.3% in weight, while in another pair the gain was 17.8. These were the extremes. The average of all the four pairs was 13.5% as given in the third column. Thus the numbers of most interest are the average percentage gains in each case and the other numbers given indicate the significance of these averages. Considering in turn the three groups, we see that Table I shows that the average percentage increase in the weight of the cord of the absorbing frog ranges from 13.5 to 25.1% and that in the groups given in this Table, the average percentage increase becomes greater as the average body weight of the frogs increases.

In comparing the effects of various conditions, therefore, frogs of the same weight should be used.

The conditions surrounding the frogs were next varied in several ways in order to determine those under which the absorption by the frog would be greatest. In Series II, the

frogs were kept up to their necks in standing water for twenty-four hours before examination. This was to insure the presence of the maximum amount of moisture in the body. The observations on this series were made August 5-7th. The room temperature at 10 a. m. was 28-29° C, and the temperature in the jar containing the absorbing frog ranged from 17-21° C. The absorbing frog was left intact for twenty-four hours before examination.

TABLE II.

	Body weight.		Percentage gain.	
	Extremes.	Average.	Average.	Extremes.
Group I 4 pairs	(20.7-31.5)	24.8	18.9%	(7.5-26.6%)

It may be noted in passing that the room temperature being high and the amount of the standing water in which the frogs were placed being only a few litres, the temperature of this water must have become rather high. Moreover, owing to the meteorological conditions prevailing on the edge of Lake Michigan from which the water supply for the laboratory is drawn, the "hot waves" in summer are accompanied by a fall in the temperature of the lake water delivered to the city, and this expresses itself in the lower temperature of the jar in which the absorbing frog was kept at this time.

In comparing the percentage increase in Series II with that for Group II of Series I, with which it may be compared, we see that the gain was slightly greater in Series II, a result which was to be expected, because the bodies of the frogs in Series II were more completely saturated with water. This difference between 15.1 %, Series I, and 18.9 %, Series II, is sufficient to warrant making arrangements in the tank so that the frogs shall always be in $\frac{1}{2}$ an inch of water, from which they cannot escape. By this means, we are assured that the frog has taken up all the water it can.

In Series III, we tried the effect of completely eviscerating the "absorbing frog" immediately after death, while in other respects the conditions for this series were essentially the same as in Series II.

Series III comprises observations on ten pairs of frogs. The absorbing frog was eviscerated immediately after death and allowed to remain in the jar for twenty-four hours. As in Series I, the results are presented in three groups, arranged according to the average weight of the frogs forming the groups.

TABLE III.

	Body weight in grams.		Percentage Gain in Absorbing Frog.	
	Extremes.	Average.	Average.	Extremes.
Group I				
3 pairs	17.6-22	19.6	14	(6.6-27.1)
Group II				
4 pairs	31.-39.2	35.1	16.9	(4.9-26.9)
Group III				
3 pairs	47.6-50.5	49.8	23	(16.7-31.6)

On comparing the average percentages for the three groups in Series III with those already given for Series I, they appear so nearly alike that we may conclude that eviscerating the absorbing frog immediately after death has no marked influence in the gain of weight by the spinal cord. This would seem to preclude the action of micro-organisms entering the body after death from the alimentary tract as a factor in increasing the weight of the cord of the absorbing frog. Up to this point, all the observations on the absorbing frog had been carried on at the temperature of the tap water or a little above it, and hence in Series IV, a much lower temperature was tried to determine the effect of reducing the temperature of the absorbing frog.

Series IV.—General Conditions—August 16-23, 1900. Both frogs of each of the thirteen pairs were normally saturated with water. The absorbing frog was eviscerated immediately after death and kept in a refrigerator at 3-10° C for twenty-four hours. Room temperature 10 a. m., 22-28° C. Records in three groups according to average body weight.

TABLE IV.

	Body Weight in grams.		Percentage Gain in Absorbing Cord.	
	Extremes.	Average.	Average.	Extremes.
Group I				
4 cases	6.8-27	17.2	19.5	(9.4-25.2)
Group II				
5 cases	32.8-42.1	37.7	20.5	(13. -27.3)
Group III				
4 cases	48.7-74.5	57.3	22.2	(17.9-25.6)

When we consider that Groups I and II in Series IV give a high percentage apparently because the cases of least absorption are still high as compared with Series III, and that Group III gives even a lower percentage in Series IV, than in Series III, despite the fact that the average body weight in the former is 57.3 grms. as against 49.8 grms. in the latter, it would appear unwise to attribute any of the differences observed to the influence of the lower temperature in Series IV.

We conclude from the foregoing four Series, that we can obtain concordant and nearly maximum results if we use "saturated" frogs of the same body weight—unopened during the period of absorption and kept at the temperature of the tap water.

We next sought to determine the effect of extracting water from the entire animal before testing the absorption of the cord.

The observations are given under Series V. In this case both frogs of each pair were put in a perfectly dry dish and there kept for twenty-four hours before they were killed. The dish was covered with a fine sieve and the temperature was that of the laboratory. At the end of twenty-four hours they were weighed a second time to determine the amount of loss of water. The four pairs had been set aside, one pair in each dish, and it is perhaps worth noting that for the two frogs of each pair the proportional loss was closely similar while the whole series of pairs gives a wide variation.

Series V—Preliminary table to show the relative loss of weight in each of the four pairs of frogs after remaining in a dry dish at the temperature of the laboratory for twenty-four hours.

TABLE V.

Pair.	Loss in Body Weight.	
	Frog Used as Control.	Frog Used for Absorption.
1	11.8%	12.4%
2	12.1%	12.7%
3	10.2%	11.7%
4	15.4%	14.9%
Average	12.4%	12.9%

The differences in the percentage loss of body weight seem most probably due to slight differences in the motion of the air over the different dishes, thus altering slightly the rate of evaporation.

We may now state the conditions for Series V. The observations were made October 16th and 17th. Both frogs of each four pairs were kept in a dry dish for twenty-four hours previous to killing. The absorbing frog was left intact in the jar at the temperature of running water—15–15.5° C. Room temperature 10 a. m., 18–22° C. Records for all the pairs taken together. The body weights are given first for the normal wet frogs and then for the same after drying.

TABLE VI.

		Body Weight in Grams.		Percentage Gain in Absorbing Frog.	
		Extremes.	Average.	Average.	Extremes.
4 pairs {	Normal	31.2–45.4	38.3	6.9%	(0.6–13%)
	After drying				
	24 hrs.	27.2–40.8	33.4		

It is to be noted here that the normal frogs had also been dried, their cords having thus lost weight by drying¹: hence the gain recorded has been calculated under the most favorable conditions for showing a large gain; for if the weight of the standard fresh frog cords had been used, the percentage gain would be much less. If we compare the percentage of gain in the spinal cord as shown by frogs of this normal body weight,

¹ In the case of two groups of heavy Bull-Frogs (Vide (1) p. 320, Table 6) the loss in the weight of spinal cord as the result of 25 hours drying amounted to 13% of the normal weight of the cord. In this connection it must be remembered that the changes in the amount of water take place very readily in the Bull-Frog.

i. e., 38.3. grams, we find that from Series III and Series IV, Group II, in each series, we might have anticipated here an average gain of 16.9 to 20.5 %, instead of which we find only 6.9 %.

It appears that when the absorbing frog has been made to take up the maximum amount of water as in Series II, III and IV, the increase in weight of cord is large—whereas when the frog has been dried for twenty-four hours previous to death, losing thereby about 12 % of its body weight mainly in the form of water, the increase in the weight of the cord is small, 6.9 %, the records for the extreme cases being reduced in correspondence with the averages. This indicates that the absorbing cord gets its fluid from the surrounding tissues.

We turn next to consider the rate at which the increase in weight takes place. All the observations thus far recorded are for the increase occurring during the single period of twenty-four hours. It is proposed now to present our determinations of the increase in the weight of the absorbing cord for 1, 2, 3, 4, 5, 6, 12, 18 and 24 hours, using a constant method of preparation so as to make the results comparable. As will be seen by looking at the accompanying table (VII), the increase is not perfectly regular, but the deviations from regularity are not large enough to suggest more than the variability to be expected in a small series of records. The general conditions under which the observations in Series VII were made were those observed in Series II.

Series VII. To show the influence of the length of time elapsing between death and examination on the weight of the absorbing cord:

TABLE VII.

Series VII. To show the influence of the length of time elapsing between death and examination, on the weight of the absorbing cord.

No. of Pairs of Frogs.	Body Weight in Grams.		Percentage increase in the Weight of Absorbing Cord		
	Extremes.	Average.	Average.	Extremes.	Time in hours.
5	18.5-23.8	19.9	5.2	2.1- 8.0	1
4	14.1-26.3	19.7	6.8	2.5-12.0	2
5	12.7-24.1	19.4	8.0	6.5- 9.2	3
5	15.5-23.0	18.7	15.5	3.3-19.9	4
5	16.3-21.4	18.4	15.6	5.5-22.9	5
4	30.0-53.2	42.8	15.8	11.9-19.6	6
5	41.5-56.5	45.9	15.4	6.8-21.8	12
4	29.6-43.0	36.8	16.8	3.2-37.5	18
5	40.8-65.1	50.7	19.6	12.8-29.5	24

On examining the foregoing table and looking in the first instance at the column showing the average increase in the weight of the absorbing cord, it appears that the smallest number is for the first hour 5.2%. For each hour after this there is an increase up to the sixth hour inclusive. After this the percentages are irregular. Moreover, in the fourth hour the percentage is 15.5%, while in the sixth hour it is but very slightly more, 15.8%. Accordingly, we infer that the most rapid absorption takes place during the first four hours.

Two features of table VII are to be particularly noted: First, the average weight of the pairs of frogs for the last four entries in the table is greater than for the first five entries. This greater weight, as well as the longer time that the cords are left after death, should have given us a much greater percentage increase in weight. That the actual figures fall short of what was to be anticipated is, in our opinion, due to the lateness of the season (from mid-October on to November 5), during which the observations for the last four periods were made. The results, therefore, for the last entry, frogs of 50.7 grms., absorbing for twenty-four hours, give us at the beginning of November only 19.6% gain, which is much below what we should anticipate when we compare it with Group 3 in Table I, observed in July. Absorption then is demonstrable at the end of an hour and takes place rapidly during the first four hours after, when it nearly reaches the maximum. Be-

yond this period, the lateness of the season makes it unwise to attempt an interpretation of this table.

Cause of the Increase in Weight.

Thus far it has not been shown that the increase in the weight of the absorbing cord is due to water, although this cause has been the one tacitly assumed. For the determination of this point the cords of those frogs used in the 6, 12 and 18 hour groups of Series VII, were utilized. In the case of each of these groups the cords were dried at 85°C after weighing, and the amount of residue (dry substance), was determined.

In the three tables which follow (tables VIII, IX and X), there are given first the average body weights for both the "control" and "absorbing" frog, the percentage gain in weight for the standard millimeter of the absorbing frog—first as directly observed, second as calculated on the basis of the dried substance—and for both control and absorbing cords, the percentages of water and the absolute weights of the dry residues.

TABLE VIII.

	Control Frog.	Absorbing Frog.
Average Body Weight in grams	44.9	40.6
Percentage Increase in the weight of the Absorbing Cord after 6 hours	{ observed calculated from dried residue }	15.8%
Percentage of Water in the Spinal Cord		14.0%
Absolute Weight of dried residue of Cord in grams	78.8%	81.6%
	0.0106	0.0105

TABLE IX.

	Control Frog.	Absorbing Frog.
Average Body Weight in grams	45.7	46.1
Percentage Increase in the Weight of this Absorbing Frog, after 12 hours	{ observed calculated from the dried residue }	15.4%
Percentage of Water in the Spinal Cord		17.9%
Absolute Weight of dried residue of Cord in grams	78.6%	83.7%
	0.0118	0.0106

TABLE X.

	Control Frog.	Absorbing Frog.
Average Body Weight in grams	37.9	35.7
Percentage increase in the Weight of the Absorbing Frog, after 18 hours	{ observed calculated from dried residue }	16.8%
Percentage of Water in the Spinal Cord	79.9%	84.7%
Absolute Weight of dried Residue of Cord in grams	0.0093	0.0084

Looking at the tables, we observe first that the percentage of water in the absorbing cord increases as the length of the time increases. The percentage of water also increases more rapidly than the increase in the weight of the absorbing cord, as there is a correlated loss in the amount of dried substance.

On estimating the moist weight of both the control and absorbing cords on the basis of the percentage value of the weight of dried substance, we find as given in the three tables under "percentage increase in the weight of the absorbing cord—calculated from dried residue," that the percentage of gain is approximately equal to the observed percentage. Theoretically, it should be exactly equal to the observed percentage, but slight inaccuracies in weighing to tenths of a milligram, which are here relatively important, will explain the discrepancies.

It seems plain, therefore, that the gain in weight of the absorbing cord is due to the imbibition of water, and that in this process solids diffuse out of the cord. Casual observations on the spinal cord of the white rat do not reveal any tendency on the part of the cord of that animal to take up water in the way the cord of the frog does. For this reason we should hardly expect this reaction to be found in other mammals.

Summary.

From these results we conclude that the gain in the weight of the absorbing cord is due to the imbibition of water, and that the cord, when taking up water, also loses in solids. In this process there is wide individual variation.

In addition to the general effect of season as expressed in

the reactions of the entire frog toward water, the conditions which distinctly modify this process are: (1) The amount of water in the body of the frog—the increase in the absorbing cord being less when the frog is dry; (2) The length of time during which the absorption is allowed to continue—the increase in the absorbing frog being greater the longer the time. (These observations do not extend beyond twenty-four hours.) (3) Finally, the weight of the frog is a factor; the larger frogs showing the greater relative increase in weight of the absorbing cord. On extending these observations, we have a few cases to show that in the bull-frog, a similar increase in the weight of the cord occurs after death, but in the mature white rat there is no evidence that this reaction occurs.

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OBSERVATIONS ON THE DEVELOPING NEURONES OF THE CEREBRAL CORTEX OF FOETAL CATS.

By SHINKISHI HATAI.

(From the Neurological Laboratory of the University of Chicago.)

With Plate XIV.

From studies on the human spinal cord, HIS ('89) in 1889 reached the following conclusions: In an early stage of the central nervous system, the germ cell divides and produces the daughter cells. Sooner or later each daughter cell sends a process from one pole towards the periphery; that is, away from the ventricle. This process is known as the earliest formation of the neuraxone. Thus the neuraxone is the first process to develop from the nerve cells or neuroblasts. Since HIS made the above observation on the spinal cord of the human embryo, it has been widely accepted by almost all investigators as a fact, and extended to the other divisions of the central nervous system.

In 1899 VON BECHTEREW made observations on the cerebral cortex of human embryos, which had been treated by the silver impregnation method. Curiously enough, the nerve cells in the earliest stage did not show the neuraxone, although the dendrites stained beautifully. From this observation he concluded that: "Die Axencylinder gehören offenbar zu den späteren Gebilden an den Nervenzellen, denn die ursprünglichen Anlagen der Nervenzellen entbehren noch ganz der Neuraxonen. Manches spricht dafür, dass die Axencylinder aus dem Kerne der Nervenzellen, dem früheren Embryonal-körperchen hervordachsen, doch bedarf dies noch der Bestätigung. Die Collateralen der Axencylinder wachsen immer später als ihre Stammfasern an den rosenkranzförmigen Anschwellungen des letzteren hervor."

VON BECHTEREW's observations were confirmed and extended by PATON in 1901, who has studied the early developmental history of the cortical layers in the foetal pig, though he did not demonstrate the structure of the process in order to explain it as a dendritic outgrowth. He considers, however, the supposed axone of previous observers as nothing more or less than a process of a spongioblast upon which the ganglion cell lies. For this reason, he decides against the axone as follows: "I do not believe that at this period the neuroblasts have any basal process or axone," . . . "there is in my opinion conclusive proof that the dendrites are the first processes of the cerebral ganglion cells to develop."

The present writer arrived at the same conclusion from the study of the developing neurones of the cerebral cortex of foetal cats. The observations were made on the same preparations which had been used for a previous investigation on the mitosis ('01) in the nerve cells; besides this foetal rats and pigs were used for comparison. The present paper deals only with the observations mentioned above, and further studies on the histogenesis of the cortex will appear later on.

Figure 1 was taken from the cross section of the cerebral cortex near the middle of the hemisphere of a foetal cat. For convenience, it is divided into six layers enumerated from the ventricle towards the periphery.

The first layer is composed entirely of primitive ectodermal cells which present a somewhat cylindrical shape. Among these spherical cells, or "germ-cells", are noticeable here and there.

The second layer is composed of spherical or oblong cells. Numerous mitotic figures are noticeable in this layer. In this second layer the outline of the cell-body is hard to demonstrate, especially in the cells which lie nearer the first layer. On the other hand the cells which lie near the third layer show a fairly distinct outline of the cell-body. This becomes clearer as we pass further and further away from the ventricles into the upper layers. The cell-bodies of the second layer are densely crowded. According to some investigators the daughter cell

sends a process towards the ventricle, and this process, sooner or later, rotates half way at or near the ventricular layer (the second layer of the present paper).

The cells in the third layer, as well as the layers above it, show a distinct outline of the cell-body and the characteristic structure of the various elements can here be seen. In this layer, the cell-bodies of both spongioblast and neuroblast are sparsely distributed as Figs. 1 and 2 show. Figure 2 shows this layer under a high magnification. The neuroblasts and spongioblasts are readily distinguishable by their size and form. The neuroblast (a) has a large nucleus and the outline of the cell-body is very distinct, while the spongioblast (b) exhibits a smaller nucleus as well as an indistinct cell outline. A most important feature which can be seen in this figure is the definite direction of the cell-process of the neuroblast. All the cell processes turn towards the periphery or cortical surface. The cells are strictly monopolar. The cytoplasm is hardly visible around the nucleus except at the one point, where the processes come out. The shape of the nucleus is variable, sometimes spherical and sometimes oblong in form. In general, the nucleus tapers towards the process. The process stains more deeply than the surrounding structures; though in some cases, one can trace the process to quite a distance, yet in most cases, it disappears abruptly, owing, very probably, to a bending at the tip.

In the fourth layer, the cell-bodies are crowded more densely than in the case of the third layer. Though one can see somewhat similar cells whose processes turn towards the periphery, yet the majority of them show a quite different arrangement as well as a more complex structure. This is shown clearly in Fig. 3, which has been drawn from this layer under a high power. In most cases, instead of being monopolar, the cell-body has distinctly two processes from its two ends, thus showing a bipolar structure. One process is exactly the same in shape and size as well as staining reaction as the process described for the cells of the third layer, while the other process is extremely delicate and much shorter than the former. It stains rather faintly. Curiously enough, in this layer the main

process in many cases turns towards the ventricle instead of the periphery, thus taking a reversed direction. This, however, can be explained as the result of the rotation of the main process, for we can see several stages in the rotation, as the figure shows. The beginning of rotation is shown at (a), and cells half rotated as well as those completely rotated, are easily found. From this, we conclude that the main or large processes of the cells in the fourth layer, which show a similar character to those in the third layer, have really the same structure and significance. The process thus rotated, however, shows quite an important morphological alteration when compared with the corresponding process in the lower layers. The terminal portion of processes enlarges greatly, and finally forms a somewhat triangular shaped expansion. From two extremities of the basal line of the triangle, very delicate branches are produced, one from each end. In some cases, the secondary branch enlarges again at its terminal points and forms other branches. The size of the terminal enlargement is variable, as will be seen from Fig. 3. Further, the processes show a somewhat irregular outline and have a variable calibre instead of tapering gradually as do those of the third layer. The nucleus in the bipolar cell is somewhat spherical, except in a very few cases; at least it does not show the oblong shape to be seen in the monopolar cells. Whether the shape of the nucleus has some relation to the movement of the cell-body, we cannot say positively, though such a relation is very probable.

The question at once arises concerning the nature of the process which first appears; whether it is a neuraxone or a dendrite. According to the existing view, this process is the neuraxone because it is the first process to develop. But as will be seen from the illustration, one can hardly regard it as the axone, since it has none of the characters of an axone. On the other hand, the terminal enlargement where two branches arise, as well as the irregular outline of the process gives it all the characters of a dendrite. Further, the second process which arises directly from the opposite side of the cell-body favors this interpretation for it shows the character of the neuraxone.

This fourth layer in the adult human cortex stained with Golgi's method reveals many cells (cells of Martinotti), the main dendrites of which run towards the ventricles, while the axone goes towards the surface of the cortex, thus exhibiting the arrangement at maturity which this method of development would lead us to expect.

The studies on the fifth layer furnish still stronger evidence. In this layer the direction of the main processes is exactly the same as in the third layer; that is, the processes turn towards the surface of the cortex. The only differences between these two layers just mentioned, are (1) shortening of the long diameter of the nucleus, (2) enlargement of the cell as a whole. Besides these important differences we observe the formation of the new processes from the base of the cell-body. This basal process newly developed, is extremely slender and similar in character to the corresponding process in the fourth layer. Partly or completely rotated cell-bodies are observed, but the number of such cells is very small; a single field (oc. 4 \times obj. 1-12 B. L.) containing one or two or sometimes none of these cells. Thus we can say that the direction of the main dendrites is the same in both earlier stages and in the adult; that is, rotation does not take place in this layer, and the main process which was produced first from the cell-body is a dendrite, the neuraxone appearing later. This is shown also in Fig. 3, where the cells already have their main processes, while the basal process or neuraxone is as yet only slightly developed. PATON ('00), who noticed a similar appearance in the cortical layer of the foetal pig, said "The process (main process or dendrite), apparently continuous with the nucleus, can be followed often well into the superficial layer. I do not believe that at this period the neuroblasts have any basal process or axone."

These observations apply also to the cortical layers of the foetal rat. The developmental history of the neurone in this animal is quite similar to that in the cat, and therefore there is no necessity to describe the rat cortex in detail.

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ILLUSTRATIONS.

PLATE XIV.

Fig. 1. Cross section of the cerebral cortex near the middle of the hemisphere of a foetal cat.

Figs. 2-4. Higher magnification of the three different levels corresponding to third, fourth and fifth layers of Fig. 1.

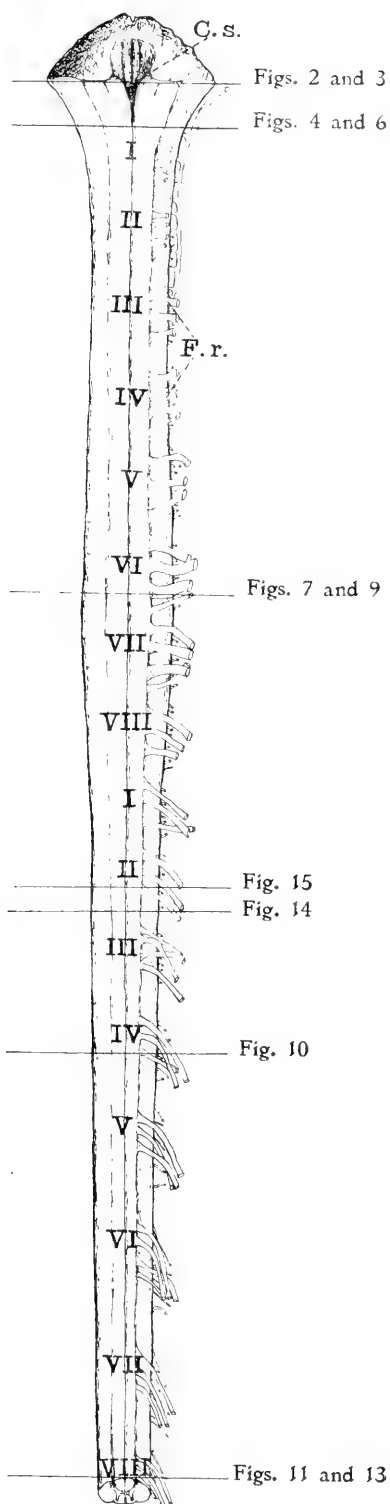




Fig. 2

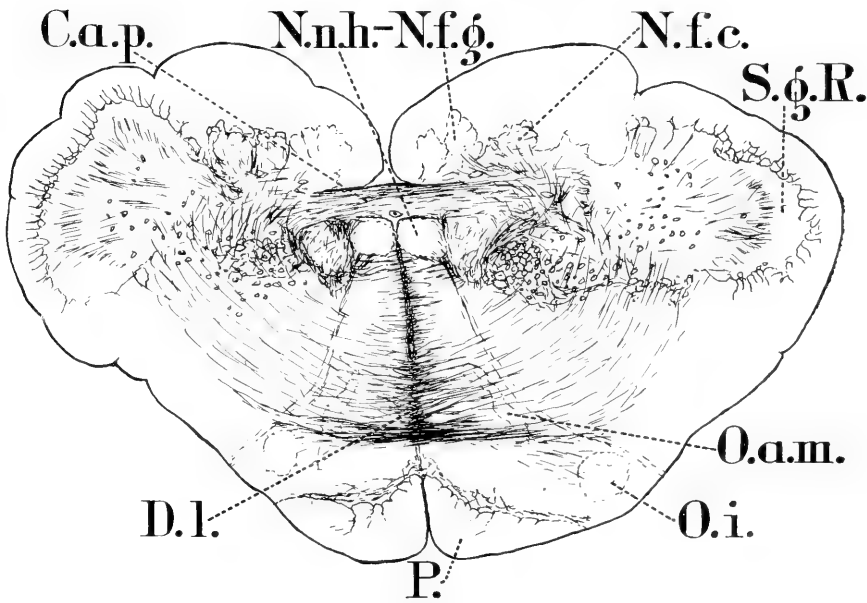


Fig. 3





Fig. 4

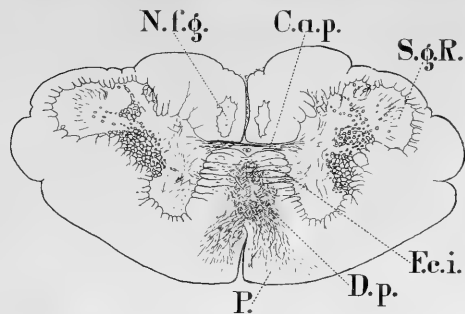


Fig. 5

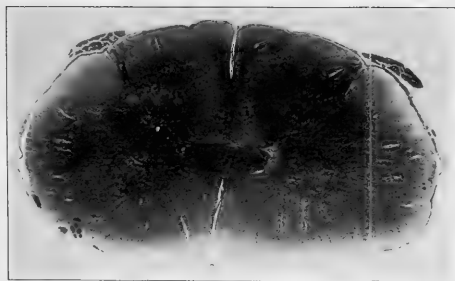


Fig. 7

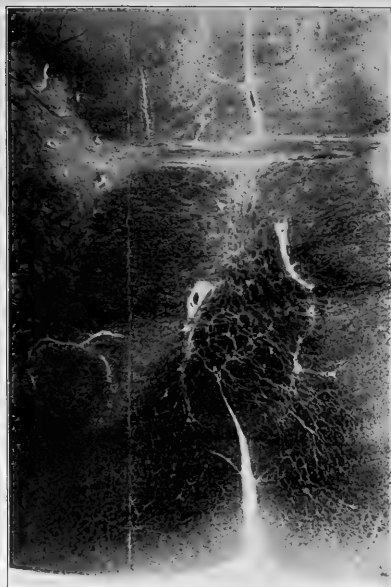


Fig. 6

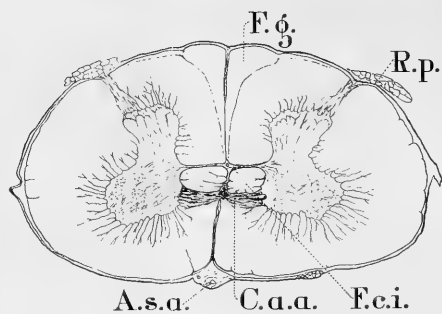


Fig. 8

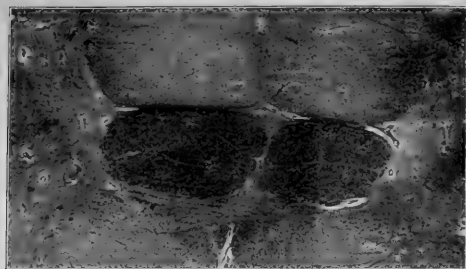


Fig. 9

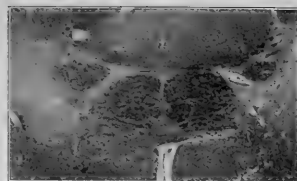


Fig. 10

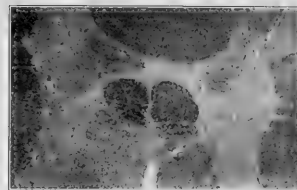


Fig. 13



Fig. 15

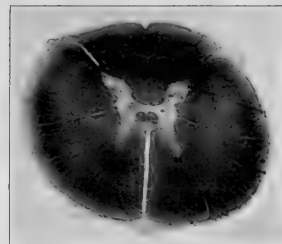


Fig. 11

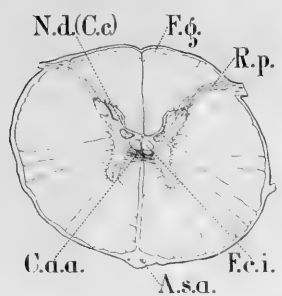


Fig. 12

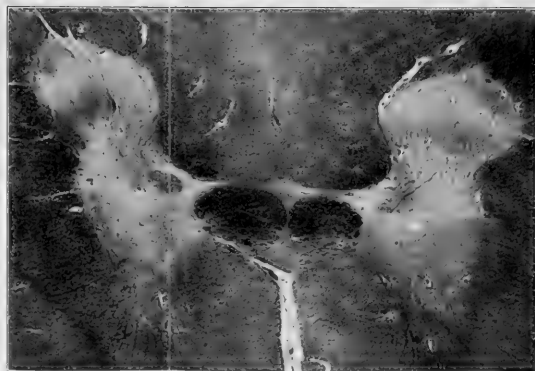


Fig. 14

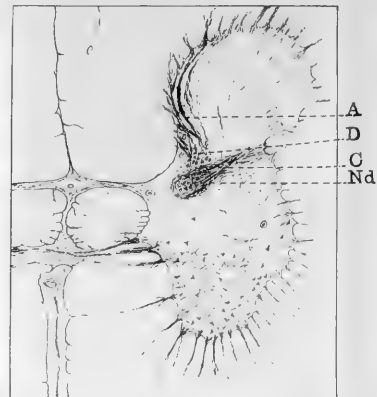
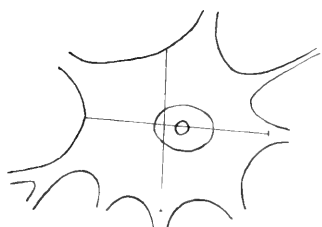
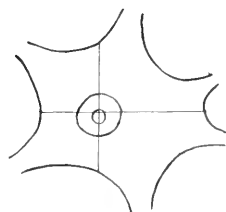


Fig. 16

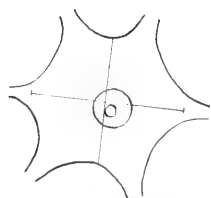




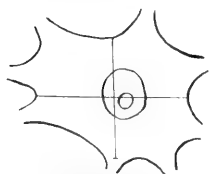
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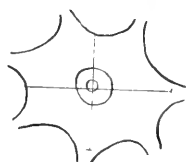
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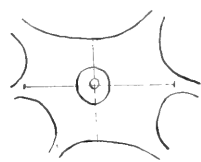
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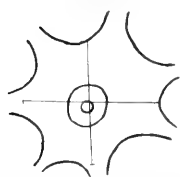
Homo
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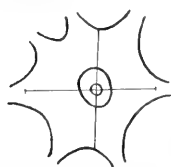
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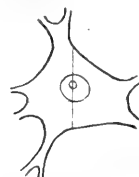
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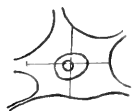
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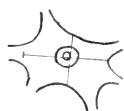
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Lepus cuniculus domesticus
44.5×36.4



Mus rattus albus
37.8×33.7



Mus musculus albus
36.8×22.9



Alalapha cinerea
31.5×28.0



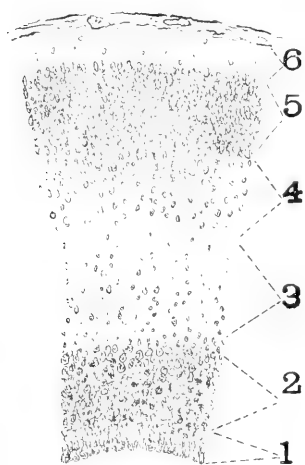


Fig. 1

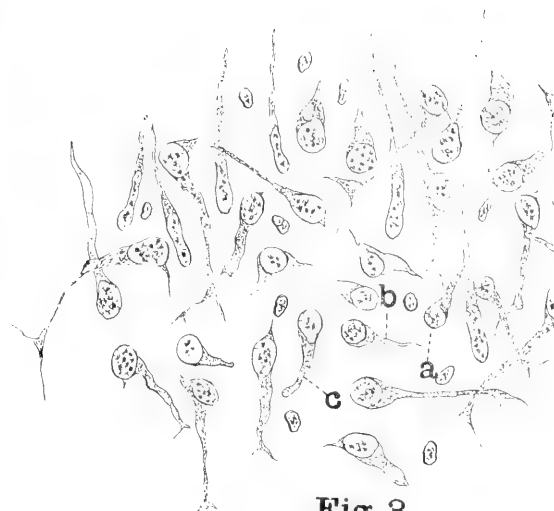


Fig. 3

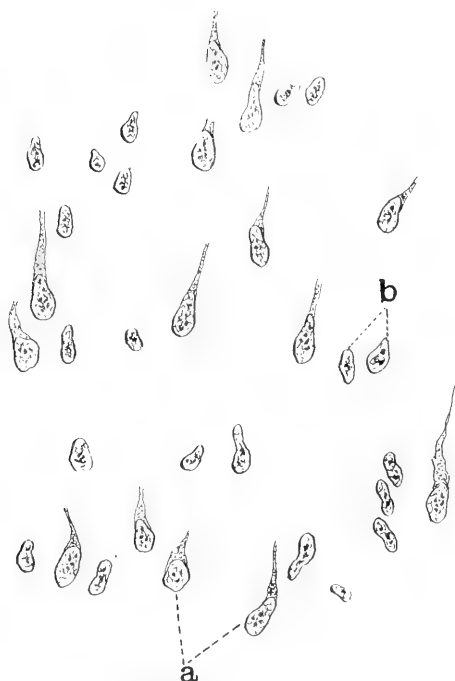


Fig. 2

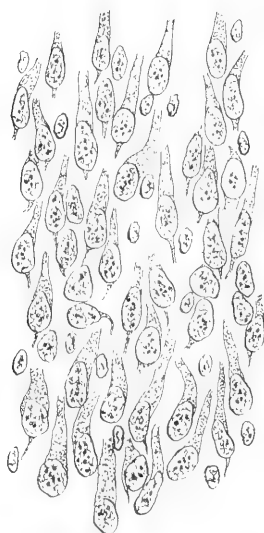


Fig. 4



THE
JOURNAL OF COMPARATIVE NEUROLOGY.

THE CRANIAL NERVES OF AMBLYSTOMA
TIGRINUM.

By G. E. COGHILL.

With Plates XV—XVI.

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INTRODUCTION.

The nervous system of *Amblystoma* has already been the subject of special microscopical studies by STIEDA ('75) and by HERRICK ('94). It has also received notice in monographs of a more general nature by OSBORN ('88), STRONG ('95), KINGSBURY ('95) and others. STIEDA made an excellent contribution to the morphology of the central nervous system, but gave little attention to the cranial nerves themselves beyond the general relations of their roots and ganglia. The studies of OSBORN and KINGSBURY concerned chiefly the central system and the nerve roots; while STRONG's observations upon *Amblystoma*, although they were made from the point of view of both the central and the peripheral relations of the neurones, were incidental to his work upon the cranial nerves of the tadpole, and were, consequently, of a fragmentary nature. HERRICK's work, alone, was offered as a systematic study of the cranial nerves of *Amblystoma* from the point of view of their central and peripheral relations. This account, however, is incomplete with reference to several important nerves and does not, Professor HERRICK authorizes me to say, represent his "present views in some matters of anatomical detail and many of morphological interpretation."

In the absence, therefore, of an accurate and comprehensive account of the cranial nerves of *Amblystoma* according to the later neurological methods, I have undertaken to ascertain the composition and distribution of all the cranial nerves, including the first two spinal nerves, and to estimate their true morphological value. The results of this investigation are presented in this paper under two main heads: Part First, which is purely descriptive; Part Second, which is a discussion of Part First in the light of recent research upon the cranial nerves of vertebrates.

My purpose in Part First is to give such a description as will be of value to those who are interested in the comparative study of the cranial nerves. This purpose demands a consid-

erable detail. For this reason a recapitulation is given which embodies the leading results without descriptive details.

My observations have been made from serial sections of *A. tigrinum*, fixed in FLEMMING'S solution and stained by WEIGERT'S method for medullated nerves. By means of these sections the nerve roots have been identified with precision. Where they enter ganglionic complexes their components have been traced through the ganglia and into the nerve trunks. When there is doubt as to the peripheral relations of root fibers it is explicitly so stated.

In Part Second I have discussed certain morphological questions which have arisen from my observations and have reviewed literature only so far as it bears directly upon these questions. A further general review would seem superfluous here in view of the recent work of STRONG ('95) and KINGSBURY ('95). These gentlemen have reviewed the literature bearing upon the amphibian nervous system in a very comprehensive manner, and since their contributions little has been added to the anatomy of the subject. Indeed, it is astonishing how meagre the available data are which contribute definitely to our knowledge of the nerve components of Amphibia. It is a remarkable fact that *Rana*, *Spelerpes* and *Amblystoma* are the only Amphibians which have been the subjects of comprehensive reports upon which comparisons can be satisfactorily based. There are many descriptions of dissections from which general inferences may be drawn, but in all such work the central relations of neurones are doubtful. Excellent as these researches may be in consideration of the methods employed in them, they are at best of little value in the solution of the present neurological questions. My reference has, therefore, been for the most part to a few recent writers upon the cranial nerves of Ichthyopsida.

In treating of the components of the cranial nerves I have used the term "general cutaneous" as applying to afferent neurones whose axones or collaterals enter the tractus spinalis n. trigemini; the term "communis," as applying to those neurones whose axones or collaterals enter the fasciculus com-

munis; the term "lateralis," as applying to the neurones which innervate the organs of the lateral line system.

In presenting these results for publication in the *Journal of Comparative Neurology*, I would express my deep obligation to the Editor, Dr. C. L. HERRICK, under whose inspiring instruction I began the research in the University of New Mexico; and to Professor C. JUDSON HERRICK for his kindly interest and helpfulness in many matters of importance. I would thank, also, Dr. H. C. BUMPUS and Professor A. D. MEAD, through whose kindness I have had for two years the liberal advantages of the Anatomical Laboratory of Brown University. I am further indebted to Brown University for the Grand Army of the Republic Fellowship during the past year.

PART FIRST.

A DESCRIPTION OF THE CRANIAL AND FIRST TWO SPINAL NERVES OF AMBLYSTOMA TIGRINUM.

I. THE OLFACTORY NERVE.

The glomeruli olfactorii in *Amblystoma* appear on the lateral side of the anterior half of the cerebral hemisphere. At the surface of the glomeruli two elements of the olfactory nerve are distinguishable. A posterior and smaller element occupies in its origin the most caudal and ventral region of the area of exit of the entire nerve, and it is separated from the anterior and larger element in the proximal portion by a double septum of the pia. The fibers of the posterior element become connected into a distinct bundle before they come in contact with the anterior element. These two elements soon unite to form the olfactory nerve and become macroscopically indistinguishable. Their respective courses can be followed farther only in exceptional cases by means of serial sections.

The anterior element takes first a lateral position in the olfactory trunk, but becomes twisted ventrad relative to the rest of the nerve by the anterior element which arises at a slightly more dorsal level; so that, as the olfactory nerve breaks up

into its terminal divisions, the fibers of the posterior element occupy the ventral part of the nerve. As the nerve approaches the nasal capsule, the anterior element separates into three divisions; one of these turns laterad and terminates in the most posterior portion of the olfactory epithelium, while the other two continue cephalad and innervate the anterior olfactory areas. The posterior element of the nerve, however, turns abruptly laterad from the point of division in the nerve and passes anteriorly of the internal nares, across the ventral surface of the olfactory epithelium, and terminates by two divisions in JACOBSON'S organ.

It is possible that some fibers of the posterior element of the olfactory nerve pass over into the anterior element during their close contact with it and through this course terminate in the olfactory epithelium proper, but there is no direct evidence of such a condition. On the other hand, comparative evidence indicates that the two elements are morphologically distinct.

II. THE OPTIC NERVE.

The optic nerve passes cephalo-laterad from the chiasma to its foramen in the lateral wall of the cranium. Beyond this it inclines a little cephalad and passes ventrally of the r. ophthalmicus profundus V, dorsally of the m. rectus internus, and into the antero-mesial side of the m. retractor bulbi. The latter muscle is inserted about the entrance of the optic nerve into the eye.

III. THE EYE-MUSCLE NERVES.

1.—*The Oculomotorius.*

The foramen of the third nerve is in the lateral wall of the cranium only a short distance posteriorly of the optic foramen. Outside the cranial cavity the relations of the oculomotorius vary greatly. Indeed, the variation is such that it is impossible to describe the nerve of any one specimen as typical. For this reason, and also because some of the variations I have observed are important in interpreting some otherwise obscure points, I give an account of several specimens with more or

less detail. The specimens used for this purpose were larvae of approximately the same size, about four and one-half inches long.

Case A.—From its foramen laterad, the oculomotor nerve follows a course approximately parallel with the optic nerve. As it approaches the r. ophthalmicus profundus V, the oculomotor divides into its superior and inferior branches.

The *superior ramus* passes dorsally of the r. ophthalmicus profundus, and following for some distance the mesial aspect of the m. rectus superior, innervates this muscle. But just at the point where the nerve begins to ramify into the muscle it comes into very close relation with a twig from the r. ophthalmicus. The trigeminal twig penetrates the m. rectus superior from the mesial side and comes to lie along the lateral and superior surface of the muscle. This case alone would indicate a possibility of an anastomosis between these two nerves at this point.

The *inferior ramus* of the oculomotor continues the course of the main nerve distally in a position ventral of ophthalmicus profundus and dorsal of the m. rectus internus. It then penetrates the m. rectus inferior from the dorsal to the ventral side. At the ventral margin of the muscle it sends one twig dorsad to the m. rectus internus which it innervates, and another twig latero-cephalad to supply m. obliquus inferior.

As the inferior ramus of the oculomotor approaches the superior surface of the m. rectus inferior in the manner just described, it comes in contact with the inferior ciliary nerve of the ophthalmicus profundus. There are no ganglion cells visible at this point, and the greater part, if not all, of the ciliary nerve separates from the oculomotorius as the latter penetrates the muscle.

Case B.—The third nerve turns cephalad from its foramen closely compressed between the temporalis muscle and the lateral cranial wall. In this position it lies parallel with the tendon of the mm. recti inferior and internus, and dorsally of the tendon. As the muscles arise from this tendon the nerve comes to lie mesially of them and divides into the inferior and superior rami.

The *superior ramus* at once becomes applied to the mesial side of the m. rectus superior, and is distributed to this muscle without coming in contact at any point with the trigeminal twig mentioned in Case A.

The *inferior ramus* passes dorsally of the m. rectus internus in two divisions. These divisions unite, however, before they come in contact with any muscle and before they give off any branches. On the dorsal surface of the m. rectus inferior the nerve comes in contact with the mesial surface of the inferior ciliary nerve and at this point of contact there are few ganglion cells. The ciliary nerve is clearly distinguishable from the oculomotor and passes laterad across the dorsal surface of the muscle while the third nerve comes to lie on the mesial side of the muscle. The branches which supply the m. rectus internus and m. obliquus inferior arise proximally of the contact with the m. rectus inferior and the branch to the latter muscle passes cephalad laterally of the m. levator bulbi.

Case C.—The *inferior ramus* passes ventrally of the m. rectus internus and becomes applied to the ventro-mesial aspect of the m. rectus inferior. From this position it sends fibers back to the ventral side of the m. rectus internus and, later, it gives off the branch to the m. obliquus inferior.

These three cases show the following essential relation of the third nerve in *Amblystoma*: (a) The m. rectus superior is innervated by the superior ramus, which passes dorsally of the r. ophthalmicus profundus. That the nerve ever anastomoses with a trigeminal twig with which it sometimes comes in contact is made entirely improbable by Case B where no such contact occurs. (b) The mm. rectus inferior, rectus internus and obliquus inferior are innervated by the inferior branch which passes ventrally of the r. ophthalmicus profundus.

The order of branching in Case B renders it wholly improbable that the rectus internus and obliquus inferior receive fibers from the fifth nerve, as would seem possible from Case A taken alone. Observations in Case B, and on other specimens also, make it improbable that this trigeminal nerve, with which the third sometimes comes in contact, has anything to do with

the innervation of the m. rectus inferior. The ciliary ganglion is transitory, and probably at no time functional.

It will be noticed, also, in these cases, that the inferior branch of the third nerve may pass either dorsally or ventrally of the m. rectus internus to reach the m. rectus inferior, that it may approach either the dorsal or ventral surface of the m. rectus inferior. Again, it may penetrate the latter muscle on its way to the m. obliquus inferior. It may or may not bear a ciliary ganglion.

2.—*The Trochlear Nerve.*

The fourth nerve emerges from the dorsal surface of the brain, near the middle line in the angle between the optic lobes and the cerebellum. It passes dorso-cephalad to its foramen in the parietal bone. Outside the foramen it passes cephalad closely compressed between the cranium and the temporalis muscle. On emerging from this position at the anterior margin of the muscle, it inclines ventrad and meets a branch of the ophthalmicus profundus. I find no positive evidence of an anastomosis in this case, although the nerves are in very intimate relation with each other. The fourth nerve is penetrated by the trigeminal twig, and then passes through the m. levator bulbi and innervates the m. obliquus superior.

3.—*The Abducens.*

The sixth nerve emerges from the ventral side of the medulla some distance posteriorly of the roots of the seventh nerve. It passes cephalad ventrally of these roots. It is usually removed some distance from the roots of the fifth, but in younger specimens it may be closely compressed against the ventral surface of these nerves. Its course lies ventrally of the trigeminal roots until it reaches the Gasserian ganglion. The abducens then becomes closely applied to the ventral surface of that part of the ganglion which belongs to the ophthalmicus profundus. It always becomes enveloped by the ganglion cells for a short distance. I find no direct evidence to show that trigeminal fibers enter the sixth nerve within the Gasserian

ganglion. The relations at this point receive further notice in the paragraphs upon the trigeminal fibers to the m. levator bulbi.

As the sixth nerve passes out of the ganglion it is usually in close relation with the r. ophthalmicus profundus. Beyond this point there is considerable variation in the behavior of the nerve. In one case it sends off two twigs each of which anastomoses with a small twig arising independently from the Gasserian ganglion. The two resulting nerves innervate the m. levator bulbi. One division of the main nerve then supplies the m. retractor bulbi while the other division innervates the m. rectus externus. In another case the twigs to the levator muscle are absent and the part of the nerve which is destined for the m. rectus externus divides. One division passes on either side of the m. retractor bulbi. In still other cases the entire nerve to the external rectus passes laterally of the retractor muscle.

4.—*Trigeminal Twigs to the M. Levator Bulbi.*

The case just mentioned, in which twigs from the fifth and sixth nerve fuse to innervate the levator muscle, demands special notice. It is evident here, either that the m. levator bulbi is innervated from two central sources, or that there is an interchange of fibers between the fifth and sixth nerves. My observations upon this and other cases will admit of no other alternative.

In contrast, however, with the variation just cited, the only fibers terminating in the levator muscle of two other heads are derived wholly from the sixth nerve. In one of these a small cluster of fibers passes from the r. ophthalmicus profundus into the abducens as the two nerves leave the cranium and while they are in close contact with one another.

In the light of this conflicting evidence, it is not absolutely certain that the entire innervation of the m. levator bulbi is by the ophthalmicus profundus, as I have implied in a previous communication (1901). It is certain, however, that all the nerve supply to this muscle cannot come from the sixth nerve,

and there is always a possibility of its entire innervation coming from the fifth nerve indirectly through the sixth. Yet, as I have already pointed out, the motor fifth root is widely separated from the sixth nerve during their course through the ganglion, and none of my preparations show any evidence of fibers passing from one into the other. The trigeminal fibers to the eye muscles cannot be explained as coming from the motor root of this nerve. They must come from the root of the ophthalmicus profundus, though I have observed but one case that gives any evidence whatever for such an hypothesis. In this case, in which motor fibers elsewhere showed a differential stain, medullated fibers could be traced continuously through the ganglion from the root to the trunk of the ophthalmicus profundus. Still, I have not distinguished motor axones entering the ophthalmicus profundus portion of the root of the fifth nerve. The exact relations, therefore, of the neurones which innervate the m. levator bulbi in *Amblystoma* are unknown.

IV. THE TRIGEMINAL, FACIAL AND AUDITORY NERVES.

A. THE ROOTS AND GANGLIA.

1.—*The Ganglia and Origin of the Roots.*

The roots of the fifth, seventh and eighth nerves leave the medulla by four distinct areas of exit. Three of these areas are at approximately the same transverse level, in which that of the lateralis VII root is dorsal; that of the motor VII root, ventral; that of the auditory and communis VII roots, between the other two. The fourth area of exit belongs wholly to the root of the fifth nerve, and is located some distance anteriorly of the other three and from the extreme lateral margin of the medulla.

The Gasserian ganglion proper, the ganglion of the anterior division of the lateralis VII root and the ganglion of the ophthalmicus profundus V form a fused ganglionic complex which is located intracranially near the anterior end of the ear capsule. The geniculate ganglion lies latero-ventrally and a

little posteriorly of the Gasserian ganglion and is separated from it by the cartilaginous base of the ear capsule. The ganglion of the posterior division of the lateralis VII root lies still farther laterad on the hyomandibular trunk near and beyond the lateral border of the ear capsule. The ganglia of the auditory roots lie at the entrance of the nerve into the ear capsule and project some distance into the capsule. The ganglion of the dorsal VIII root is closely compressed against the posterior face of the ganglion of the ventral VIII root.

2.—*The Root of the Trigeminus.*

The fibers of the motor V component appear in the ventro-lateral margin of the cinerea, some distance caudad of the exit. From this position they turn latero-ventrad and emerge from the postero-ventral portion of the area of exit of the entire nerve. They at first occupy a ventro-lateral position in the root, but as they approach the ganglion they come to lie dorsally of that part of the root which belongs to the r. ophthalmicus profundus. Within the ganglion the motor component inclines laterad and issues from the ganglion as the postero-ventral portion of the r. mandibularis.

The general cutaneous portion of the trigeminus forms into two divisions some time before it reaches the ganglion. One of these divisions lies dorsally of the motor component and the other ventrally of it. However, these two divisions are closely compressed together about the motor component, and the line of division between them is not always perceptible. In one series of sections, in which the motor nerves are elsewhere well differentiated, there appear a few medullated fibers which seem to pass directly through the ganglion and enter the r. ophthalmicus profundus. The significance of these fibers has been discussed in connection with the innervation of the m. levator bulbi. The dorsal division of the ganglion, the Gasserian ganglion proper, gives rise to two nerves: from its lateral portion, the general cutaneous component of the mandibular trunk; from its mesial portion, the general cutaneous portion of the infraorbital trunk. The latter component is generally known as

the r. maxillaris V, but in applying this term to the nerve in *Amblystoma* I use it in a restricted sense discussed in Part Second of this paper.

3.—*The Lateral Line Root.*

The area of exit of the lateralis VII root is divided into four sections. Counting from the dorsal side, the first and third sections are well separated from each other and project farther caudad than either of the other two. The second section lies chiefly between the first and third although it projects farther cephalad than either. The fourth section lies close to the antero-ventral margin of the third and extends farther cephalad and ventrad than any of the other sections. From the first and third of these sections arises the posterior division of the lateralis VII root which enters the truncus hyomandibularis VII; from the second and fourth sections arises the anterior division of the same root which enters into relation with the trigeminus. The neurones of the second section form the r. ophthalmicus superficialis VII; those of the fourth section form the r. buccalis VII. It is evident, therefore, that the neurones of the rr. ophthalmicus superficialis and buccalis tend to enter the medulla farther cephalad than do those of the truncus hyomandibularis.

As the anterior division of the lateralis VII root emerges from the medulla, it becomes compressed between the medulla and the most dorsal and anterior portion of the posterior division of the root. It does not at any point come in contact with the auditory roots or with the motor or communis roots of the facialis. It begins to separate from the posterior division of the lateralis root at about the transverse level of the exit of the trigeminal root. In older specimens, it comes at the same time into contact with the latero-dorsal side of the root of the trigeminus, but in younger larvae it is compressed against the lateral margin of the dorsal rim of the medulla and cerebellum to near the Gasserian ganglion. The ganglion of this root lies on the dorsal surface of the Gasserian ganglion. The two ganglia are so fused together that it is difficult to distinguish them even with the aid of serial sections.

The posterior division of the lateralis VII root, immediately after its exit, comes in contact with the fibers of the dorsal VIII root as they enter the brain. Having passed cephalad of the latter root it immediately comes in contact with the dorsal side of the communis VII root, as the most anterior fibers of the latter emerge from the brain and while the lateral margin of the lateralis root is still in contact with the dorsal VIII root. For a short distance beyond this point the lateralis root becomes separated from the communis VII and dorsal VIII roots, but when the latter has turned laterad into the ear capsule the lateralis root assumes like relations with the ventral VIII root and the communis VII root.

As the two divisions of the lateralis root separate from each other, the posterior division comes in contact for the first time with the motor root of the facialis which at this level has come to lie laterally of the communis root. The three roots then turn laterad together into the foramen of the facialis, which penetrates the antero-ventral portion of the ear-capsule. At the distal opening of this foramen the lateralis component enters its ganglion from which arise the axones of the r. mentalis VII.

4.—*The Auditory and Communis Roots.*

From the area which is between the exits of the lateralis and motor VII roots, three roots arise; the dorsal and ventral VIII, and the communis VII. The two larger and posterior sections of this area belong to the auditory roots. The section belonging to the dorsal VIII projects slightly farther caudad than that of the ventral VIII. The contiguous margins of these two sections diverge anteriorly and the section belonging to the communis VII is wedged in between them. It extends, also, dorsad anteriorly of the dorsal VIII section, and it lies dorsally of the anterior portion of the ventral VIII section.

The dorsal auditory root projects laterad and a little cephalad into its ganglion. The ventral VIII inclines cephalad ventrally of the communis VII, dorsally of the motor VII and mesially of the dorsal VIII root. It at length passes around the anterior margin of the ganglion of the dorsal auditory root

into its ganglion. The neurones of the dorsal auditory root form the r. acusticus sacculi; those of the ventral auditory root, the r. acusticus utriculi. The peripheral relations of these rami have been fully described by HERRICK ('94) and need no farther notice in this paper.

The communis root of the facialis turns from its exit immediately cephalad, mesially of the dorsal VIII root, ventrally of the lateralis VII root and dorsal of the ventral VIII root. As the latter root inclines laterad the communis root comes to lie mesially of it, and in contact ventrally with the motor root of the facial. As the communis root turns laterad into the foramen it lies mesially and anteriorly of the motor VII. The position of the geniculate ganglion, from which the axones of the communis root arise, has been described on page 215.

5.—*The Motor Root of the Facialis.*

The motor root of the facial nerve issues from the medulla alone, ventrally of the anterior portion of exit of the auditory roots. It becomes at once applied to the ventral surface of the ventral VIII root, near the medulla. It holds this relative position until the ventral VIII root turns laterad, when it meets the communis root mesially of the ventral VIII root. It later comes to lie laterally and posteriorly of the communis root and ventrally of the lateralis root. It crosses the postero-lateral portion of the geniculate ganglion to enter the hyomandibular trunk, and continues laterad in this trunk ventrally of the lateralis root and its ganglion and dorsally of the communis component of the trunk.

B. THE RAMI OF THE TRIGEMINAL AND FACIAL NERVES.

1.—*The Ramus Ophthalmicus Profundus V.*

The general course of the r. ophthalmicus profundus is cephalad and a little laterad from its ganglion, dorsally of the proximal portion of the m. retractor bulbi and mesially of the distal portion. It passes dorsally, also, of the m. rectus inferior and m. rectus internus and of the optic nerve, and ventrally of the m. rectus superior. In the region of the optic nerve the ophthalmic divides into three terminal branches.

Where the ophthalmicus profundus comes into close relation with the m. retractor bulbi it gives off ventrally the *inferior ciliary nerve* (not figured). On the surface of the retractor muscle the inferior ciliary nerve sometimes comes in contact with the sixth nerve, but this relation seems accidental. A little farther along its course, ventrally of the ophthalmicus profundus, it comes in relation with the inferior branch of the oculomotor as described on page 212. From this point the ciliary nerve may continue along the surface of the rectus inferior to the insertion of the muscle, or it may lie entirely apart from this muscle, until it approaches the eye-ball. A part of the nerve enters a foramen in the sclera under the insertion of the m. rectus inferior, beyond which the fibers could not be definitely traced. The rest of the branch continues laterad between the sclera and the surrounding fascia to the margin of the sclerotic cartilage, and there enters the eye.

The *second branch* (o. p. V. 2.) of the ophthalmicus profundus is given off dorsally at about the same level as the first. It passes cephalad dorsally of the main nerve to the margin of the temporalis muscle where it divides. One of the nerves resulting from this division is the superior ciliary (not figured). It may come in contact with the superior branch of the third nerve as described on page 6, and then follow the m. rectus superior to the eyeball, or it may pass freely from the point of branching to the insertion of the rectus superior, under which it enters a foramen in the sclera. In some cases, and perhaps as a rule, this division penetrates the m. rectus superior.

The other division of the second branch of the ophthalmicus profundus is a *cutaneous nerve*. It turns dorsad around the lateral margin of the m. rectus superior and then cephalad along the dorsal surface of the muscle it inclines dorso-mesiad and divides. The anterior of the two resulting twigs passes to a position mesial of the r. ophthalmicus superficialis VII. It sends a few fibers cephalad but the larger part of the twig turns caudad to the skin over the cranium near the mid-dorsal line. The other twig of the cutaneous branch passes directly caudad

laterally of the twig just described to the skin over the temporalis muscle mesially.

In the immediate vicinity of the optic nerve several twigs arise which may be considered together as the *third branch* (o. p. V. 3) of the ophthalmicus profundus. They may be described regardless of their order of branching, as follows: *Twig "A"* passes to a position mesial of the r. ophthalmicus superficialis VII and then cephalad to the skin over the anterior part of the cranium. *Twig "B"* is distributed to the skin immediately dorsally and anteriorly of the eye. *Twig "C"* penetrates the fourth nerve on the mesial side of the m. levator bulbi, then penetrates the muscle also and goes to the skin of the immediate vicinity of the dorsal margin of the muscle. It sends fibers mesiad, also, to the skin, in the vicinity of the r. ophthalmicus superficialis VII. *Twig "D"* sends fibers to the immediate vicinity of the upper eyelid and then passes across the r. ophthalmicus superficialis VII to the skin in the region of that nerve.

In one specimen a large twig from the third branch of the ophthalmicus profundus penetrates the roof of the nasal capsule and anastomoses with a twig of the mesial terminal branch of the nerve. The resulting nerve passes again through the cartilage to the skin over the capsule.

It should be emphasized that there is great variation in the manner in which the twigs described above arise from the main nerve or from one another. They may arise as two or more distinct nerves, a part of one fusing with a part of the other and then branching again in an indefinite manner. Their point of origin from the main nerve is also variable, and in consequence of this the general direction of the twigs is in no way constant. The area innervated, however, by all collectively seems constant, i. e. the skin of the infra-orbital region, and for a variable distance cephalad and caudad of this region.

The terminal branches, also, of the r. ophthalmicus profundus vary in their manner of origin from the main nerve. The three may arise simultaneously, or the ventral branch may arise from the lateral branch. I have observed no case in which the ventral arises from the mesial branch. The ventral branch is

essentially constant in its peripheral relations, but the other two show so wide variation that it is impossible to describe any particular case as typical.

The *mesial terminal branch* (*m. o. p. V.*) of the r. ophthalmicus profundus passes cephalad mesially of the olfactory epithelium near the dorsal roof of the nasal capsule. Within the capsule the branch gives off numerous twigs which pass dorsad to the skin. In one specimen seven of these twigs penetrate the cartilaginous roof of the ear capsule by distinct foramina. One of these comes in close contact with the r. ophthalmicus superficialis VII but never anastomoses with it. Another may anastomose with a division of the third branch of the main nerve. In one specimen a large division of the mesial branch passes laterad across the dorsal surface of the olfactory epithelium and fuses with a division of the lateral terminal branch of the main nerve. The resulting nerve goes to the skin laterally of the external nares.

Within the nasal capsule the mesial branch comes in contact with a large branch of the olfactory nerve and remains closely compressed against its surface for some distance, but there is no interchange of fibers between the two nerves. The differential myelin stain by the side of the non-medullated fibers of the olfactory nerve makes this relation perfectly clear.

The distribution, then, of the mesial terminal branch of the ophthalmicus profundus is to the skin over the anterior part of the nasal capsule anteriorly to the tip of the snout and lip, and from the mid-dorsal line to some distance laterally of the external nares.

The particular relation which the *lateral terminal branch* (*l. o. p. V.*) of the ophthalmicus profundus may assume with the mesial terminal branch has already been mentioned. It innervates the skin of the snout and lip laterally and posteriorly of that innervated by the mesial terminal branch, as far as the anterior canthus of the eye. Its fibers frequently come in close relation with the r. buccalis VII, but there is no anastomosis between the two nerves.

The *ventral terminal branch* of the ophthalmic nerve (*v. o.*

p. V.) turns ventrad from its origin from the main nerve, then a little laterad ventrally of the olfactory epithelium. It divides near the transverse level of the posterior end of the internal nares. The smaller twig arising from this division turns abruptly laterad posteriorly of the internal nares and anastomoses with the lateral division of the r. palatinus VII (*l. p.*). As the resulting nerve approaches the lateral border of the internal nares it sends a small twig caudad while the rest of the nerve turns cephalad and innervates the epithelium of the antero-lateral portion of the roof of the mouth. The larger division of the ventral ophthalmic branch passes cephalad and soon anastomoses with the mesial division of the r. ophthal-palatinus VII (*mp.*). This nerve passes along the mesial aspect of the internal nares and becomes compressed between the vomerine bone and the overlying cartilage. It sends fibers to the epithelium between the vomerine bone and the premaxillary.

2.—*The Truncus Infra-orbitalis.*

The infra-orbital trunk passes laterad from the Gasserian ganglion between the masseter and temporalis muscles to the lateral border of the latter, then cephalad ventrally of the lateral part of the eye. It contains lateralis neurones of the anterior division of the lateralis VII root, and general cutaneous fibers from the mesial part of the Gasserian ganglion. The point and extent of fusion of these components are exceedingly variable. They may fuse immediately upon leaving their ganglia, in which case the general cutaneous component occupies an antero-ventral position in the trunk; or they may not fuse until they turn cephalad about the border of the temporalis muscle. In one case I find the truncus mandibularis fused with the truncus infra-orbitalis to near the lateral border of the temporalis muscle, and this fusion is as complete as that at any point between the typical components of the trunk.

Near the flexure of the infra-orbital nerve about the border of the temporalis muscle it gives off a twig of fibres from both components to the skin of the immediate vicinity. Other small twigs, also, seem to be always given off in this region. As the

nerve approaches the eye it gives off a general cutaneous twig to the skin posteriorly of the eye, and a similar twig to the under eyelid. Large fibers, also, are given off along the course of the nerve to the post-orbital and infra-orbital sense organs.

The exact position of the nerve relative to the eye varies, apparently, according to age. In younger larvae it lies ventrally of the extreme lateral border of the eyeball, while in older specimens it approaches the mid-ventral region of the eye.

At the transverse level of the eye the infra-orbital trunk divides into the r. buccalis VII (*b. VII.*) and the r. maxillaris V (*mx. V.*) (The term maxillaris is used with limitations discussed in Part Second.) The r. buccalis, continuing cephalad, follows the outer and dorsal border of the maxillary and pre-maxillary bones, ventrally of the external nares, to near the middle line of the snout. Along the distal part of its course it comes into close relation with twigs of the ophthalmicus profundus, but fuses with none of them. The terminal fibers of this nerve have not all been traced to their termination, but they have the appearance of lateralis fibers and there are lateral line organs along the course of the nerve. Moreover, the region it traverses is liberally supplied with general cutaneous fibers from the r. ophthalmicus profundus. Comparative evidence, also, is in harmony with my conclusion that the r. buccalis is a purely lateral line nerve (*v.* Part II).

The *maxillaris V* turns laterad from the point of division of the infra-orbital nerve. Although it passes cephalad of the transverse level of the eye, it extends at the same time into the large ventrally projecting fold of the upper lip. The area it innervates is postero-ventral of that innervated by the lateral terminal branch of the ophthalmicus profundus V.

It is possible that there are a few lateralis fibers carried out a short distance in the r. maxillaris, but I can discover no constant arrangement of this kind.

3.—*The Ramus Ophthalmicus Superficialis VII.*

The r. ophthalmicus superficialis VII arises from the ganglion of the anterior division of the lateralis VII root, dorsally of

the lateralis component of the truncus infra-orbitalis. It inclines more dorsad than the latter nerve and turns cephalad about the border of the temporalis muscle. Its further course is subcutaneous, mesially of the eye, to the tip of the snout. There appears to be no constant manner of branching, but numerous twigs arise all along its course and go to sense organs arranged over, and on either side of, the main nerve. It is a purely lateral line nerve.

4.—*The Truncus Mandibularis V.*

The mandibular trunk of the trigeminus arises from the dorso-lateral portion of the Gasserian ganglion and from the motor V root. The direction of the earlier part of its course varies with age. In the adult it inclines caudad; in the larvae, cephalad. In either case it at first lies between the masseter and temporalis muscles, to both of which it sends large motor twigs (not figured).

While passing between these two muscles, the mandibular nerve gives off its *first cutaneous branch* (*mbd. 1.*). This branch passes latero-dorsad across the lateral aspect of the truncus infra-orbitalis, then caudad over the lateral aspect of the masseter muscle and m. depressor mandibulae, and some distance caudad beyond these muscles. It is distributed to the skin over the parts mentioned.

The mandibular nerve now penetrates the m. masseter and emerges subcutaneously laterally of the muscle, in the region of the mandible. In this vicinity the nerve divides in an irregular manner. A nerve of considerable size, the *second cutaneous branch* (*mbd. 2.*), may arise within the m. masseter and emerge from it independently, or it may arise after the main nerve has emerged from the muscle. It sends one or more twigs to the skin about the angle of the jaw, and another (*mbd. 2.a.*) cephalad to the inner epithelium of the cheek.

On approaching MECKEL'S cartilage the mandibular V sends off its *third cutaneous branch* (*mbd. 3.*). This passes cephalad laterally of the ramus of the jaw, at first dorsal then ventrally of the r. mentalis externus VII. These two nerves

frequently come in contact with each other but they never anastomose. The trigeminal branch innervates the skin along the lateral aspect of the mandible, and extends nearly to the tip of the chin. It tends to lie more ventrally of the mandible in the distal part of its course.

The mandibular trunk now follows the dorsal border of MECKEL'S cartilage for a short distance cephalad. It then gives off the *fourth cutaneous branch (mdb.4)* which continues the course of the main nerve, sending fibers to the neighboring skin, and at length becomes enclosed in a canal between the dentary bone and MECKEL'S cartilage. Within this canal it gives off fibers which probably terminate in the teeth. It anastomoses by one twig with the r. alveolaris VII, and with another passes out of the canal and becomes subcutaneous along the lateral margin of the mandible. The latter twig innervates the skin of the under lip to the symphysis mentis.

The remainder of the mandibular nerve turns ventrad from the last point of branching, and passes between the angular bone and MECKEL'S cartilage. It then passes mesad ventrally of the mandible and soon breaks up into three divisions. Two of these divisions, the most anterior and the most posterior one, contain both motor and general cutaneous fibers. The middle division contains only general cutaneous fibers. Various twigs from these divisions anastomose with one another, but there seems to be no constant arrangement in this regard. An anastomosis between a terminal twig of the posterior division and the terminal fibers of the r. jugularis VII seems to be constant. The fibers united in this manner almost immediately enter the m. interhyoideus. The other motor fibers of the mandibular V in the lower jaw are distributed to the m. mylohyoideus; the cutaneous fibers to the skin ventrally of this muscle. It is a noticeable feature of these nerves that they always lie on the ental side of the lateral line nerves of the same region.

5.—*The Truncus Hyomandibularis.*

The hyomandibular trunk of the facialis passes laterad from the geniculate ganglion through the large foramen in the base

of the ear capsule. It contains all the motor VII fibers, communis fibers from the geniculate ganglion and lateralis root fibers. At the lateral border of the ear capsule it bears the lateralis ganglion and divides into three large rami.

The ramus mentalis (mtl. VII.) contains all the lateralis fibers of the hyomandibular trunk. It inclines a little caudad and then turns ventro-cephalad along the suspensorium between the m. masseter and m. depressor mandibulae nearly to the angle of the jaw. As it emerges from between these muscles it divides into two nerves of about equal size, the r. mentalis externus and the r. mentalis internus.

The r. mentalis externus (mtl.ex.) gives off twigs to the sense organs about the angle of the jaw, and posteriorly of this, and passes cephalad laterally of MECKEL's cartilage to the symphysis. It innervates the lateral line organs which are arranged in an irregular manner along its course. Its relation to the third cutaneous branch of the mandibular V has already been mentioned as only that of contact.

The r. mentalis internus (mtl. in.) passes ventrad from the point of division of the main nerve, across the lateral side of the m. depressor mandibulae at its insertion. It then turns inward ventrally of the mandible and divides into two about equal branches which diverge slightly and then pass parallel with each other to near the symphysis. The distribution of the entire nerve is to lateral line organs along its course.

Besides the two main branches of the r. mentalis, there are small twigs given off between the m. masseter and the m. depressor mandibulae. These pass directly out to sense organs over the muscles.

The r. jugularis VII (jgl. VII) carries out all the motor component of the hyomandibular trunk. It immediately inclines caudad and meets the r. communicans IX + X ad VII, from which it receives its general cutaneous component. The nerve then enters the m. depressor mandibulae, innervating it by several large twigs, and emerges from its posterior border. From this position the jugularis turns cephalad and inward subcutaneously, ventrally of the branchial musculature. It innervates

the m. interhyoideus and the overlying skin. Its most anterior fibers fuse with the terminal twig of the mandibular V as already described.

The r. alveolaris VII, composed wholly of communis fibers, follows the posterior border of the suspensorium to the angle of the jaw. Along this part of its course the r. alveolaris lies mesially of the hyo-suspensorial ligament and anteriorly of the deep pharyngeal evagination which represents the embryonic spiracular cleft. At the ventral end of the suspensorium the nerve passes across the mesial side of the angle of the jaw and enters its canal in the mandible.

Sometime before the alveolaris emerges from this canal it divides into two branches, one of which anastomoses with the fourth cutaneous branch of the mandibular V, and continues cephalad within the canal to the teeth and gums, while the other passes out of the canal at about the transverse level of the internal nares, and passes inward to the epithelium of the floor of the mouth.

In some cases the r. alveolaris gives off a large branch near the angle of the jaw. This branch enters a distinct canal in the mandible and has a distribution similar to that of the main nerve.

Soon after leaving the hyomandibular trunk, the main nerve receives fibers from the r. communicans IX + X ad VII. This relation will be noticed further in connection with the latter nerve.

Facialis A.—As the hyomandibular trunk leaves the foramen there is given off from the communis component a small twig which passes caudad closely compressed upon the ventral side of the ganglion of the r. mentalis. From this point it continues latero-caudad, ventrally of the r. communicans IX + X ad VII, to the region of the posterior extremity of the ceratohyal bar. Here it anastomoses with the r. pre-trematicus IX. This nerve appears in but one of my specimens. It will be discussed in Part II as *Facialis A.*

In two specimens I have found a second cluster leaving the hyo-mandibular trunk just after its exit from the foramen. These

fibers are exceedingly fine and seem to come from the communis component. They pass cephalo-laterad between the m. masseter and m. depressor mandibulae in close relation with a twig of the r. mentalis and are distributed to the skin over the muscles just mentioned. They can not be traced to sense organs. Although I have not been able to demonstrate this twig in every case, it would be quite possible for its fibers to become obscured in some branch of the r. mentalis and for them to have their typical distribution without being demonstrable.

6.—*The Ramus Palatinus.*

The r. palatinus VII arises from the proximal portion of the geniculate ganglion and inclines ventrad into the roof of the mouth. It then continues cephalad and a little laterad, across the ventral border of the m. retractor bulbi, to the transverse level of the posterior end of the internal nares. Here the nerve forms into two terminal branches. The mesial branch (*m.p.*) passes cephalad mesially of the internal nares and receives the mesial division of the ventral terminal branch of the ophthalmicus profundus. The lateral terminal branch (*l.p.*) of the palatine turns abruptly laterad from the point of division just behind the internal nares and fuses with the lateral division of the ventral terminal branch of the ophthalmicus profundus. At the junction of the two nerves there is a prominent cluster of ganglion cells. The peripheral relations of these terminal branches of the palatine nerve have been described in connection with the r. ophthalmicus profundus.

From near the point of branching the palatine nerve sends branches also mesiad to the epithelium posteriorly of the vomers. Other branches are given off in the earlier course of the nerve and are distributed to the epithelium of the roof of the mouth on either side of the nerve. Twigs of these branches anastomose frequently and some of them fuse with twigs from JACOBSON'S anastomosis. Other fibers from the r. palatinus may fuse with the r. palatinus caudalis.

The r. palatinus, in one of my specimens, shows remark-

able variation in the manner of origin from the geniculate ganglion. It leaves the ganglion by two divisions of about equal size. One of these passes dorsally, and the other ventrally of the m. retractor bulbi. Beyond the muscle the two divisions of the nerve fuse into a common trunk which does not differ in any other respect from the typical palatine nerve.

7.—*The Ramus Palatinus Caudalis.*

The r. palatinus caudalis arises from the distal portion of the geniculate ganglion. It may penetrate the cartilage into the roof of the mouth only a little way from the foramen of the r. palatinus. On the other hand, it may be fused with the hyomandibular trunk nearly to the distal end of the foramen. In one case it leaves this trunk near the opening of the foramen and passes caudad in a foramen of its own in the cartilage of the latero-ventral border of the ear-capsule. It emerges from this foramen at the anterior margin of the fenestra ovalis. In other cases, two nerves penetrate into the roof of the mouth by distinct foramina and function, apparently, as the r. palatinus caudalis.

Soon after the nerve emerges from its foramen it unites with the second ramus of the ninth nerve to form JACOBSON'S anastomosis. From this fusion the enlarged nerve passes cephalad in the roof of the mouth about to the transverse level of the optic foramen and in a position approximately ventral of the r. ophthalmicus profundus V. It sometimes receives twigs from the r. palatinus.

8.—*Accessory Trigeminal Twigs.*

Besides the main rami of the fifth nerve there are, in some specimens, two small caudad nerves which arise independently from the Gasserian ganglion or from the general cutaneous component of the infra-orbital trunk soon after it leaves the ganglion. When they do not appear independently they are probably incorporated into some of the branches of infra-orbital nerve. I distinguish them as the *first* and *second accessory twigs* of the trigeminus (not figured).

The first accessory twig arises from the Gasserian ganglion

with the most dorsal and mesial fibers of the general cutaneous component of the infra-orbital trunk but is entirely distinct from this component as this nerve leaves the ganglion. It follows along at first the anterior, and then the dorsal side of the infra-orbital nerve, but inclines more dorsad than the latter and passes to a subcutaneous position over the border of the m. temporalis. As it approaches the skin it divides. Each of its two divisions soon fuses with a twig from the infra-orbital trunk. One of the nerves thus formed passes nearly to the mid-dorsal line and innervates the skin over the ear capsule. The other nerve passes to the skin farther cephalad. It meets a twig from the r. ophthalmicus superficialis VII, but seems to separate from it intact.

The second accessory twig of the trigeminus arises from the general cutaneous component of the infra-orbital nerve as this component unites with the lateralis component to form the main trunk. It is compressed for a short distance against the posterior side of the infra-orbital nerve, but soon turns latero-caudad dorsally of the lateral portion of the ear-capsule. It is distributed to the skin over the proximal portion of the squamosal bone.

V. THE GLOSSOPHARYNGEUS AND VAGUS.

A. THE ROOTS AND GANGLIA.

The ninth and tenth nerves arise by five roots which enter a common ganglionic complex at the posterior end of the ear capsule. The parts of this complex which belong to the different roots are very closely compressed together and it is not always possible to determine the dividing lines between them. By a study of several sets of serial sections cut in various planes I have determined the mutual relations of the different ganglia and the course of nearly all the components through them. The motor components of the different roots were traced especially in a preparation where the motor and lateralis fibers alone were well medullated. As no motor axones emerge with the lateralis root, the motor components of the other roots, with one ex-

ception, could be traced conclusively. The peripheral relations of the motor axones of the third root of the vagus are doubtful.

1.—*The Lateral Line Root.*

The first or most anterior root of this complex is the *lateralis root* of the vagus (X.I.). It arises at about the same horizontal level with the origin of the *lateralis VII* root, and but a short distance posteriorly of the latter. The root inclines caudad and rapidly ventrad until it comes in contact with the dorsal surface of the root of the *glossopharyngeus*. It then continues directly caudad closely compressed upon the ninth nerve, and comes in contact with the emerging second root of the vagus. In some older specimens, however, this contact does not take place. As the *lateralis X* root enters the ganglion it comes to lie mesially of the root of the ninth, but remains perfectly distinguishable from the second root of the vagus with which it sometimes comes in contact.

The ganglion of the *lateralis* root forms the most dorsal portion of the ganglionic complex. In the anterior part of the ganglion a small division extends laterad about the border of the ear capsule and emerges as the *r. supratemporalis X*. A second division projects latero-caudad and gives rise to the *lateralis* component of the *r. auricularis vagi*. The remainder of the ganglion extends caudad along the dorsal surface of the complex and gives rise to the *lateralis* axones which are more or less fused with the *r. visceralis vagi*.

2.—*The Root of the Glossopharyngeus.*

The root of the ninth nerve emerges from the medulla at a transverse level immediately posterior to the exit of the *lateralis* root of the vagus, but from the extreme lateral border of the medulla ventrally of the latter root. It is composed of *communis* and motor fibers. The motor fibers, in reaching the surface of the medulla, pass across the ventral side of the *fasciculus communis* at the point where the *communis* component of the nerve leaves the *fasciculus*, and the two components emerge from the medulla as a single root.

Upon leaving the medulla the root of the ninth nerve (IX) comes in contact with the ventral side of the lateralis root of the vagus and holds this relation with it until the two nerves approach the ganglion. The root of the ninth then passes more laterad than the other, and enters the anterior portion of the ganglionic complex. Its ganglion extends ventrad and laterad and forms the anterior end of the complex. It supplies the communis component of the truncus glossopharyngeus. The entire motor component also enters this trunk.

In the older larval stages and in the adult the two roots just described leave the cranium by a distinct foramen of their own. In these stages, also, the ganglion of the glossopharyngeus extends a considerable distance out on the trunk and seems to have a tendency to become constricted off from the rest of the complex.

3.—*The Second Root of the Vagus.*

The second root of the vagus leaves the extreme lateral border of the medulla at a transverse level which is considerably posterior of the exit of the ninth nerve. It is composed of motor and communis fibers. It turns caudad and meets the third root of the same nerve just before entering the ganglionic complex. As the two roots enter the complex the second root passes dorsally of the third, while its ganglion lies ventrally of the lateralis ganglion and posteriorly of the ganglion of the glossopharyngeus.

The motor fibers, at the proper stage of myelination, may be traced through the complex from the second root of the vagus into the first and second branchial trunks of the vagus. The communis component of these trunks is also derived from this root. It is impossible, however, to say whether neurones of this root enter the truncus visceralis. The ganglion of the root seems to extend caudad and send fibers into the truncus visceralis, but it is possible that this caudal extension of the ganglion belongs to the communis component of the third root of the vagus.

4 — *The Third Root of the Vagus.*

The third root of the vagus varies greatly in its manner of origin from the medulla. It may leave the medulla by one large root or by several rootlets. It receives a large component from the tractus spinalis n. trigemini, a small component from the fasciculus communis, and a small motor component. The communis component forms the cephalic part of the root, and the motor fibers form the caudal portion. In some cases these two components appear as separate rootlets. The large, general cutaneous component itself may leave the brain by several rootlets. The large root, thus formed, passes directly laterad into the ganglionic complex, of which its ganglion forms the ventral portion. As already mentioned, the ganglion of the communis component probably fuses with that of the second root and is comprised of neurones from the truncus visceralis. The general cutaneous ganglion, then, forms the most ventral portion of the ganglionic complex.

The fibers which arise from the most cephalic portion of the general cutaneous ganglion pass laterad through the ventral part of the complex and enter the truncus glossopharyngeus. They form only a small portion of the trunk, and occupy the caudal part in cross section. A second cluster of fibers from this ganglion ascends in the complex between the fibers of the glossopharyngeus and those of the second root of the vagus, and go out with the r. auricularis X. The rest of the general cutaneous neurones enter the first two branchial trunks of the vagus.

The course of the motor component of this root is obscure because of its close relation with the fourth vagus root. It probably accompanies the fourth root through the ganglionic complex and enters the truncus visceralis.

5.—*The Fourth Root of the Vagus.*

The fourth root of the vagus arises singly or by as many as five distinct rootlets. The axones are first visible as ascending longitudinal fibers in the lateral column of the cord and medulla. They turn abruptly laterad from this tract and

emerge from the medulla at its extreme lateral margin. This root, in some cases, becomes closely applied to the caudal side of the third root of the vagus as the latter leaves the medulla, but, in other cases, it meets the third root near the ganglion. As it comes in touch with the ganglion it turns caudad partially embedded in the mesial portion of the complex. At the transverse level of the origin of the branchial trunks of the vagus, the fourth vagus root begins to turn laterad into the complex, and beyond this point can be traced as a continuous fiber band among the ganglion cells until it enters the truncus visceralis, of which it forms the motor component. It is probably accompanied, however, by the motor component of the third root, as described above.

B. THE RAMI OF THE VAGUS AND GLOSSOPHARYNGEUS.

1.—*The Truncus Glossopharyngeus.*

The glossopharyngeal trunk arises from the latero-ventral angle of the anterior portion of the IX+X ganglionic complex. It contains all the neurones of the glossopharyngeal root and a small general cutaneous component from the third root of the vagus.

The general course of the nerve (*IXt.*) varies greatly. In the adult it turns abruptly cephalad around the lateral border of the ear capsule and then turns caudad to the first branchial arch. In the larvae it passes laterad, to the m. levator arcus branchii primi. It usually penetrates this muscle, but in some cases it passes around the posterior end of this muscle to reach the distal end of the first branchial arch. When it penetrates the levator muscle it passes caudad laterally of it, across the lateral surface of the first epi-branchial bar, then ventrad between the bar and the m. cerato-hyoideus externus. It then passes cephalad into the first branchial arch.

The r. communicans IX+X ad VII (com. IX+X ad VII) arises from the glossopharyngeal trunk immediately outside the ganglion. It is made up of general cutaneous and communis fibers. It passes cephalad around the lateral border of the ear capsule, then laterally of the suspensorio-stapedial ligament. A

few small fibers from the nerve seem to terminate in this ligament, and others are given off in the same vicinity which seem to terminate upon blood vessels. As the nerve approaches the rami of the hyomandibular trunk it divides; one division enters the r. jugularis, while the other passes across the surface of this nerve and enters the r. alveolaris.

As to the composition of the respective divisions of the r. communicans IX+X ad VII there can be little doubt. The ramus certainly contains general cutaneous and communis fibers, and it affords the only possible source of the general cutaneous fibers already demonstrated in the r. jugularis VII. The branch to this nerve, then, must be general cutaneous in function. Furthermore, the fibers which enter the r. alveolaris have the appearance of communis fibers. In one case I have distinguished the two components from the ganglion nearly to the point of branching, but here the nerve twists in such a manner as to obscure the relations further. However, from this observation alone, it would seem probable that the whole communis component enters the r. alveolaris, for this distinctness of the components through nearly the entire extent of the nerve indicates that there would not be a mixing of the components in the division of the nerve.

In a specimen two inches long the branch of the r. communicans to the r. alveolaris consists of only a few fibers, but in older larvae and in the adult it is a nerve of considerable size. It is not demonstrable in all series of sections cut in the transverse plane, since its relation with the r. jugularis is such as to obscure its course. In series cut parallel with the sagittal plane the relation is perfectly clear.

There is frequently a recurrent motor twig from the r. jugularis which passes caudad some distance closely compressed upon the r. communicans and then enters the m. depressor mandibulae. This would give to the r. communicans, by superficial examination, the appearance of sending fibers into the muscle, but there is no anatomical evidence of the presence of motor fibers in this nerve.

The second ramus (IX,2) of the glossopharyngeus, com-

posed entirely of communis fibers, leaves the trunk a little beyond the last point of branching. It passes cephalad and a little laterad immediately beneath the ear capsule nearly to the anterior border of the latter. Here it meets the r. palatinus caudalis VII and forms JACOBSON'S anastomosis as described on page 230. This branch sends twigs also laterad to the epithelium of the pharynx. Some of its exceedingly small twigs may fuse with the twigs of the r. palatinus VII, or with the r. alveolaris VII. Such twigs, however, have been observed in but one instance.

The r. *pre-trematicus* IX (*prt. IX*) arises either separately near the second branch or by fibers derived from both the second branch and the main trunk. It is a small nerve of small thinly medullated fibers. Its course is latero-cephalad, ventrally of the m. depressor mandibulae, to the caudal end of the hyoid bar. Here it sometimes anastomoses with *facialis* "A" (see page 228). The nerve then enters the hyoid arch in a position dorsal of the mesial margin of the cartilage. It continues far cephalad in this position and seems to innervate the taste buds with which the region is liberally supplied, although no absolute contact with them has been observed.

In the region of the first m. levator arcus branchii, the glossopharyngeus gives a motor branch (not figured) to this muscle. A little farther on it sends a small *fifth ramus* (IX, 5) ventrad a short distance to anastomose with the r. *pre-trematicus* of the first t. branchialis vagi.

As the glossopharyngeus begins to turn ventrad to enter the gill arch, it sends off the *sixth ramus* (IX, 6) which continues caudad laterally of the distal portion of the first epibranchial bar and anastomoses with the fifth ramus of the first t. branchialis vagi. The general appearance of this nerve, and the fact that it is the only possible avenue for a typical distribution of the general cutaneous fibers known to be in the trunk at this point, lead me to believe that this is a purely general cutaneous nerve. A comparison with a corresponding ramus of the second t. branchialis vagi, also, seems to substantiate this view. Before the nerve fuses with the branch of the vagus, it sends fibers to the skin over the base of the first external gill.

As the t. glossopharyngeus turns cephalad into the first branchial arch, it gives off a *motor branch* (*IX, 7*) to the first m. depressor branchii; and beyond this the trunk is considered as the r. post-trematicus IX (*pst. IX*). It contains motor and communis fibers. It passes cephalad in a position lateral of the ventral portion of the first epibranchial bar and crosses the dorsal surface of the m. ceratohyoideus internus. It innervates this muscle (*IX, 8*), and in the same region sends a twig (*IX, 9*) laterally of the cartilage to the epithelium of the pharyngeal side of the bar. The terminal ramus finally turns abruptly dorsad anteriorly of the branchial cartilage to the dorsal side of the hypohyal, and distributes itself to the epithelium overlying the anterior part of the hyoid and branchial cartilages.

2.—*The First Truncus Branchialis Vagi.*

The first t. branchialis vagi (*X, 1br.*) leaves the ganglion of the IX+X a little posteriorly of the glossopharyngeus and immediately in front of the second branchial trunk, or these two trunks may arise together. The general course of the first trunk is latero-caudad across the ventral side of the second m. levator arcus branchii, then along the lateral surface of this muscle to the distal end of the first epibranchial bar, caudally of which it gives off three important branches, and beyond this branching enters the second branchial arch.

The r. pre-trematicus (*prt. X, 1*) of this trunk arises a short distance from the ganglion. It is of about the same size as the r. pre-trematicus IX. It inclines slightly caudad to the dorsal end of the first branchial cleft, in front of which it extends along the dorsal border of the first epibranchial bar. As the nerve enters the branchial arch, it receives the fifth ramus of the glossopharyngeus. The resulting nerve is distributed to the epithelium of the pharyngeal side of the distal portion of the bar.

A *pharyngeal ramus* (*X, 1br. 1*) arising either with the r. pre-trematicus or near it, passes cephalo-mesad ventrally of the ganglion IX+X to the epithelium of the pharynx. From the pharyngeal ramus there sometimes arises a third exceedingly fine twig (not figured) which anastomoses with the r. pre-tre-

maticus of the second t. branchialis vagi. A motor branch (not figured) passes from the main nerve to the second m. levator arcus branchii.

One of the three branches formed near the distal end of the first epibranchial bar is the *fifth ramus* (*X, ibr.5*), which descends into the first external gill, innervates the m. levator branchii and the m. adductor branchii, and receives the sixth ramus of the glossopharyngeus. In the distal portion of the external gill the nerve follows closely the large blood vessels, to which a large number of its fibers seem to be distributed.

At this same point of branching, a *sixth ramus* (*X, ibr.6*), also, passes caudad to anastomose with the third ramus of the second t. branchialis vagi. It corresponds to the sixth ramus of the glossopharyngeus and is probably a general cutaneous nerve.

As the branchial trunk turns cephalad into the gill arch, it sends a *motor branch* (*X, ibr.7*) to the second m. depressor branchii, and beyond this becomes the r. post-trematicus (*pst. X, 1*) which is motor and communis in function. It assumes a position laterally of the ventral margin of the second epibranchial bar. Soon after entering the arch, the nerve sends a twig (*X, ibr.8*) to the pharyngeal side of the bar. The r. post-trematicus then continues cephalad to the region of the m. interbranchiales, to which it sends a motor twig (*X, ibr.10*). In the region of this muscle there is also a twig (*X, ibr.9*) which passes across the lateral aspect of the cartilage to the epithelium of the bar. A little further cephalad the nerve divides into two terminal twigs, one of which ascends on the lateral and the other on the mesial side of the bar to the epithelium covering the proximal portion of the second branchial arch.

3.—*The Second Truncus Branchialis Vagi.*

The second branchial trunk (*X, Br.2*) of the vagus leaves the ganglion just posteriorly of the first trunk, or fused with the latter for a short distance. It inclines more caudad than the first, across the ventral side of the third m. levator arcus branchii, then caudad subcutaneously to enter the third branchial arch.

When the first and second branchial trunks of the vagus are found fused for some distance from the ganglion, there appears to be a fusion, also, of the pharyngeal rami of the two nerves. The relations of the r. pre-trematicus, also, of the second trunk become obscured. However, there are cases, in which the trunks are sufficiently separated to show that there is a pharyngeal ramus of the second trunk corresponding to that of the first, and a very small r. pre-trematicus which enters the second branchial arch and, in some instances, fuses with a third ramus of the first trunk at the dorsal end of the second branchial cleft.

As the main nerve turns ventrad to enter the gill arch, its *third ramus* (*X, 2br. 3*) passes into the second external gill and fuses with the sixth ramus of the first trunk. This nerve is distributed as is the corresponding nerve of the first external gill. From the same point of branching of the main nerve, two rami pass caudad into the third external gill; one (not figured) follows the blood vessels, while the other (*X, 2br. 4*) passes into the dorsal surface of the external gill. The latter innervates the third m. levator branchii, and sends fibers to the skin over this muscle. This nerve in some specimens, and probably in all at a particular stage of development, anastomoses with the branchial ramus of the second spinal nerve. As the external gill degenerates, the general cutaneous component of this nerve, as well as the branch from the second spinal, seems to disappear.

As the second branchial X trunk turns cephalad into the gill arch, the remainder of its motor component (*X, 2br. 6*) goes out in the ramus to the third m. depressor branchii. Beyond this point, the r. post-trematicus, in contrast with the other post-trematic rami described above, contains only communis fibers. Otherwise, it is like those rami in manner of branching and distribution (*X, 2br. 7 = X, 1br. 8*; *X, 2br. 8 = X, 1br. 9*).

4. *The Ramus Supratemporalis Vagi.*

The r. supratemporalis X (*spt.*) is the smallest nerve arising from the ganglion IX+X. It goes out of the dorsal and most anterior region of the ganglion, and inclines cephalad

around the border of the ear capsule, then dorsad along the border of the m. extensor dorsi communis. Ventrally of this muscle, however, the nerve divides. One of its divisions (*spt. 1*), passing more cephalad than the other and sometimes penetrating under the insertion of the m. extensor dorsi communis, innervates lateral line sense organs located well towards the middle line of the head over the posterior moiety of the ear capsule. The other division (*spt. 2*), passing either dorsally of or through the first m. levator arcus branchii, innervates lateral line organs at about the same transverse level as those innervated by the first division but located farther laterad.

5.—*The Ramus Auricularis Vagi.*

The r. auricularis (*aur.*) leaves the ganglion from the latero-dorsal margin and at a transverse level between the first branchial trunk of the vagus and the truncus glossopharyngeus. In the adult, however, it arises farther caudad than the second branchial trunk of the vagus. It is composed of lateralis fibers from the first vagus root, and general cutaneous fibers from the third vagus root.

A short distance from the ganglion the r. auricularis forms into two divisions, both of which are like the main nerve in composition. The areas innervated by the two components of the nerve approximately coincide. The anterior division of the nerve (*aur. 1*) extends dorsad and cephalad over the posterior two-thirds of the ear capsule and laterad to the side of the head. A general cutaneous nerve from this division (*aur. 1, a.*) extends caudad nearly to the base of the first external gill. The posterior division of the nerve (*aur. 2*) is distributed to the region which lies immediately behind that of the first division. The sense organs innervated by the lateral line components of both divisions are somewhat irregularly arranged in groups throughout the area of distribution of the nerve.

6.—*The Ramus Lateralis Superior Vagi.*

The r. lateralis superior (*l.s.*) arises from the ganglion more or less in union with the truncus visceralis. It sometimes forms the dorsal part of the latter trunk for a short distance. It is

derived wholly from the caudal projection of the ganglion of the first root of the vagus.

The *dorsal division* of the r. lateralis superior (*l.s.d.*) arises from the main nerve a short distance from the ganglion and inclines slightly laterad and abruptly dorsad between the m. extensor dorsi communis and the m. cucullaris. Near the transverse level of the axilla it begins to send fibers to the line of sense organs of the dorsum.

The main part of the r. lateralis superior follows a course dorsally of, and approximately parallel with, the t. visceralis X, but soon becomes separated from the later nerve by the m. basi-scapularis. Dorsally of this muscle it continues caudad beyond the suprascapula and innervates the sense organs of the lateral line of the trunk.

7.—*The Truncus Visceralis Vagi.*

The t. visceralis (*usc.*) passes out of the posterior extremity of the ganglion IX+X. It is composed of lateralis fibers dorsally; of motor fibers from the fourth, and probably also from the third, vagus root, ventrally; and of communis fibers in its central portion. There is no evidence of general cutaneous fibers in the trunk. The communis fibers are derived from the third root of the vagus. It may be that the second root of the vagus, also, sends some fibers into this trunk, since the latter contains the equivalent of a typical branchial trunk minus the fibers which would go to an external gill, and since the second root of the vagus affords the corresponding components of the two anterior branchial trunks of the vagus.

The t. visceralis passes caudad and slightly ventrad until it approaches the transverse level of the origin of the third spinal nerve. Here it turns ventrad across the lateral aspect of the pharynx and divides into three terminal branches.

In its course caudad, the t. visceralis usually passes between the m. basi-scapularis and the m. cucullaris. In a specimen of *A. punctatum* two inches long, however, the entire nerve inclines laterad and comes to lie on the lateral side of the m. cucullaris, and laterally also of the anterior part of the m.

dorso-trachealis. It then penetrates this muscle from the antero-lateral to the postero-mesial side, and crosses the anterior border of the m. cucullaris as the latter passes downward across the pharynx. This variation occurs in the nerve of one side only.

The *first ramus* (*usc. 1*) of this trunk arises near the ganglion from the ventral and lateral portion of the nerve. It sends fibers (*usc. 1a.*) directly to the muscle cucullaris, and also fibers through this muscle to the m. dorso-trachealis. It will be remembered that the fourth root of the vagus, the axones of which emerge from an ascending lateral tract in the cord and medulla, enter the most ventral part of the t. visceralis. From this region of the nerve, immediately outside the ganglion, the fibers go out which innervate the m. cucullaris. In origin and distribution, therefore, these fibers function as N. accessorius.

The larger, fine fibered portion of the first branch, however, inclines laterad anteriorly of the m. cucullaris and continues caudad laterally of this muscle. Early in its course the nerve gives a twig to the epithelium of the pharynx (not figured); later it sends a large number of fibers to the third and fourth mm. levatores arcuum (not figured). From this nerve there arises, also, a typical r. pre-trematicus (*prt. X₃.*) which passes along the mesial side of the third epibranchial bar and enters the third branchial arch. In one specimen, a small twig from the second t. branchialis vagi, corresponding to the fifth ramus of the glossopharyngeus, also entered this arch close to the r. pre-trematicus. In this specimen, also, a twig from the first ramus of the t. visceralis entered the fourth branchial arch, corresponding in its distribution with the fifth ramus of the glossopharyngeus.

Near the m. levator arcus, this nerve sends a twig of small fibers, probably communis, to the strip of epithelium which joins the epithelium of the fourth branchial arch with that of the pharynx. The larger, terminal portion of the nerve, however, passes between the fourth m. levator arcus branchii at its insertion and the m. dorso-trachealis, then across the mesial aspect of the caudal tip of the fourth epibranchial bar. From

this position it turns ventrad and cephalad into the fourth branchial arch, ventrally of the bar. It ultimately ascends along the lateral side of the bar to the epithelium of the dorsal surface. This terminal branch of the nerve corresponds to the first intrabranchial divisions of the first (*X, 1br. 8*) and second (*X, 2br. 7*) branchial trunks of the vagus.

The *ramus lateralis inferior* arises as a terminal branch of the t. visceralis. It turns ventrad along the lateral aspect of the pharynx posteriorly of the remainder of the trunk, and inclines slightly cephalad in close relation with the r. recurrens X. It then turns caudad and passes across the ental aspect of the coracoid plate at the level of the glenoid fossa. From this position it sends a twig mesiad which penetrates the pectoralis muscle and innervates a small group of lateral line organs of the pectoral region. The remainder of the ramus may penetrate the pectoralis muscle, or it may pass posteriorly of this muscle to innervate the line of sense organs running caudad from the axilla.

In some cases the r. lateralis inferior assumes intricate relations with the branchial nerves in the axillary region, but in other cases it is entirely removed from these nerves, so that there is no possibility of its having a motor function.

As the t. visceralis turns ventrad across the pharynx, it gives off, also, the r. intestinalis (*int.*). This nerve continues caudad and forms into three divisions. One of these divisions follows the lateral wall of the trachea to the lung. The other two are distributed to the oesophagus. A few of the fibers of the r. intestinalis are thinly medullated, but by far the greater part of the nerve is made up of fibers which appear non-medullated in WEIGERT preparations. It is impossible to say to which of the vagus roots the neurones of the r. intestinalis belong. However, since the communis neurones of the second vagus root have to do, largely if not wholly, with the branchial trunks, it seem probable that those of the r. intestinalis belong to the third vagus root.

Beyond the origin of the r. intestinalis, the t. visceralis becomes the r. recurrens (*rec. X.*). It passes cephalad in the

space between the m. sterno-hyoideus and the m. hyo-trachealis, in close relation with the ventral rami of the first and second spinal nerves. Near the flexure cephalad, the r. recurrens gives off a twig (*rec. 1*) which penetrates the m. hyo-trachealis and innervates the constrictor and dilator muscles of the glottis. This twig may send fibers, also, to the m. hyo-trachealis and m. dorso-trachealis.

At the transverse level of the glottis, the r. recurrens sends a twig (*rec. X, 2.*) of thinly medullated fibers laterad, which enters the fourth branchial arch and turns cephalad ventrally of the cartilage. It then turns dorsad on the lateral side of the cartilage and innervates the dorsal epithelium of the gill arch. It corresponds in its distribution to the second sensory intra-branchial division of the post-trematic rami of the branchial trunks of the vagus (*X, 1br. 9* and *X, 2br. 8*).

At various intervals along its course the r. recurrens sends fibers to the m. hyo-trachealis; and along its terminal portion to the m. interbranchiales (*rec. X, 3*). Anteriorly of the tracheal muscle, the terminal fibers of the nerve ascend along the mesial side of the fourth branchial cartilage to the epithelium of the floor of the pharynx. These fibers function as the terminal portion of the typical post-trematic ramus.

VI. THE FIRST TWO SPINAL NERVES.

The first spinal nerve arises by two ventral roots. The second root leaves the ventral side of the cord at the transverse level of the posterior end of the fourth ventricle. The first root arises some distance anteriorly of this. The two roots pass out of the neural canal together through a foramen in the first vertebra.

The first ramus of the first spinal nerve (*sp. 1, r 1*) leaves the nerve immediately outside the foramen. It passes cephalad ventrally of the musculature and crosses the dorsal surface of the ganglion IX+X. It is distributed to the anterior portion of the m. extensor dorsi communis.

The ventral ramus (*sp. 1 v.*) leaves the nerve at about the same level as the first ramus. It inclines ventrad and caudad

through the *m. intertransversales*, to which it sends numerous fibers. Emerging ventrally of this muscle, it sends fibers to the *m. basi-scapularis* and continues caudad in the roof of the pharynx. It turns cephalad ventrally of the pharynx, posteriorly of the *t. visceralis* and *ramus recurrens vagi*. In close relation with the latter nerve and with the ventral branch of the second spinal nerve, it lies for some distance along the dorsal surface of the *m. sterno-hyoideus*. However, upon separation from this nerve it inclines ventrad along the lateral side of this muscle and, at the transverse level of the glottis, meets the ventral branch of the second spinal nerve again and anastomoses with it. The resulting nerve innervates the *m. sterno-hyoideus* and *m. genio-hyoideus*.

In the adult the anastomoses between the ventral rami of the two spinal nerves takes place immediately as the *ramus* of the first passes out of the *m. intertransversales*. In the adult, also, the roots of the first spinal nerve seem to remain distinct in their passage through the foramen, and the axones of the second root seem to enter the ventral *ramus*. This would indicate that the axones of the second root, only, function as hypoglossal nerve. Yet the ventral *ramus* sends fibers to the *m. intertransversales*. It is possible that the fibers to this muscle, however, pass from the first into the second root in the passage through the foramen. But even if this distinctness of roots exists, the root which functions as hypoglossal would still arise as a typical spinal root, since the two roots do not differ in this regard.

After giving off the two *rami* just described, the first spinal nerve turns dorsad (*sp. 1d.*) and bears a small ganglion on its lateral side (*g. sp. 1*). The nerve then divides into two portions, one of which passes dorso-cephalad and the other dorso-caudad into the *m. extensor dorsi communis*.

The ganglion of the first spinal nerve gives rise to small medullated fibers which go out with the dorsal *rami*, and from these *rami* fibers may be traced, in one of my series, to the skin of the dorsum. These fibers to the skin must be derived from

the ganglion, though there appeared to be no dorsal root of the nerve.

The second spinal nerve arises by two or more ventral rootlets which fuse into a common root, and by a large dorsal root. The latter arises considerably caudad of the ventral root. In the adult, the dorsal root passes out of the spinal canal through a foramen in the second vertebra. From the foramen it inclines cephalo-ventrad into its ganglion, which is elongated in the same direction. The motor root, emerging from the intervertebral space, meets the cephalo-ventral end of the ganglion.

The *ventral ramus* (*sp. 2 v.*) of this nerve is made up of motor and general cutaneous fibers. Its course through the m. intertransversales, to which it sends fibers, is like that of the first spinal nerve. Ventrally of this muscle, it sends fibers to the m. thoraci-scapularis. Proximally of the anastomosis with the second spinal nerve, excepting in the adult, this nerve sends off its entire cutaneous component to the skin of the pectoral region and to the skin anteriorly of this (*sp. 2, v, a.*). Proximally of the anastomosis, also, the main nerve sends fibers to the m. sterno-hyoideus.

The *dorsal rami* of the second spinal nerve have a large general cutaneous component. In other respects they do not differ from the dorsal rami of the first spinal. There is, also, a small ramus which extends cephalad into the muscles, which probably corresponds with the first ramus of the first spinal nerve.

The *branchial ramus* of the second spinal nerve arises from the cephalic tip of the ganglion and penetrates the musculature laterad, and emerges in the vicinity of the t. visceralis X. Here it inclines caudad and dorsad, covered by the m. cucullaris and later by the m. dorso-trachealis. It finally penetrates the latter muscle and divides. One division of the nerve is distributed to the skin of the dorsum. The other division innervates the skin covering the base of the third external gill, and extends into the dorsal portion of this gill as a general cutaneous nerve. It anastomoses in some larvae with a general cutaneous branch of the second t. branchialis vagi. The

resulting nerve is distributed to the skin of the upper surface of the third external gill. This anastomosis is probably characteristic for larvae of certain stages, but in individuals with the external gills much reduced in size the anastomosis does not occur, and the branch to the external gill is very small.

VII. RÉSUMÉ OF PART I.

The element of the olfactory nerve which innervates JACOBSON'S organ arises from the postero-ventral portion of the area of exit of the entire olfactory nerve. It is fused for a considerable distance with the element which innervates the olfactory epithelium proper. None of the branches of the olfactory nerve receive medullated fibers from the trigeminus.

The innervation of the muscles of the eye is from four sources: from the third, fourth and sixth nerves, and from the r. ophthalmicus profundus V. The superior ramus of the third nerve supplies the m. rectus superior; the inferior ramus, the recti inferior et internus and the obliquus inferior. The obliquus superior is innervated wholly by the fourth nerve. The sixth nerve innervates the m. rectus externus and m. retractor bulbi. The central relation of the neurones which innervate the m. levator bulbi can not be stated positively, but they appear to be derived from the r. ophthalmicus profundus V.

The auditory nerve arises by two roots. The lateralis VII root, arising dorsally of the latter, forms into an anterior and a posterior division. The ganglion of the anterior division is on the dorsal surface of the Gasserian ganglion and gives rise to the r. ophthalmicus superficialis VII and the r. buccalis VII. The ganglion of the posterior division is on the hyomandibular trunk, near the lateral border of the ear capsule. It gives rise to the r. mentalis VII. The communis VII root arises dorsally of the ventral VIII root and anteriorly of the dorsal VIII root. It bears the facial ganglion which gives rise to the r. palatinus, r. palatinus caudalis, r. alveolaris, and sometimes to a small nerve to the r. pre-trematicus IX. The motor VII root arises ventrally of the others and enters the hyomandibular trunk.

The trigeminus arises by a single large root of motor and sensory fibers. It bears the Gasserian ganglion and the ganglion of the ophthalmicus profundus which form a common ganglionic mass with the ganglion of the anterior division of the lateralis VII root.

The r. ophthalmicus superficialis VII arises as an independent nerve wholly from the ganglion of the anterior division of the lateralis VII root, and innervates the supra-orbital group of sense organs. The r. buccalis arises wholly from the same ganglion and forms a part of the t. infraorbitalis. It innervates the infraorbital groups of sense organs. The r. mentalis VII forms into an internal and an external division. The external innervates the oral group of sense organs; the internal, the gular group. The main nerve sends fibers also to the sense organs over the region of the suspensorium.

The r. ophthalmicus profundus V gives out two ciliary nerves, which vary greatly in their peripheral relations, and several cutaneous branches in the region of the optic nerve. One of the latter meets the fourth nerve but does not anastomose with it. The lateral and mesial terminal branches of the nerve innervate the skin mesially and anteriorly from the eye; the ventral terminal branch anastomoses by two divisions with the r. palatinus VII. The general cutaneous portion of the infra-orbital trunk arises from the Gasserian ganglion and innervates the region posteriorly and ventrally of the eye, and the projecting fold of the posterior part of the upper lip. The sensory part of the mandibular trunk arises from the same ganglion. It sends one cutaneous branch caudad over the suspensorium, others to the skin about the angle of the jaw, and one to the inner epithelium of the cheek. One branch is closely associated with the r. mentalis externus along the ramus of the jaw, but does not fuse with it. Another branch anastomoses with the r. alveolaris VII within the alveolar canal of the mandible. The terminal cutaneous branches innervate the skin covering the m. mylohyoideus. The general cutaneous fibers which are found in the r. jugularis VII are derived from the third root of the vagus and are distributed to the skin cov-

ering the m. cerato-hyoideus externus and the m. inter-hyoideus.

The motor component of the trigeminus goes out with the mandibular trunk and innervates the masseter, temporalis, and mylo-hyoid muscles. A few terminal twigs fuse with fibers of the r. jugularis VII, and enter the m. inter-hyoideus. The motor component of the facial nerve innervates the m. depressor mandibulae, m. cerato-hyoideus externus, and m. inter-hyoideus.

The r. palatinus VII, near the internal nares, forms into two divisions, both of which fuse with divisions of the ventral terminal branch of the ophthalmicus profundus V. The r. palatinus caudalis passes to the roof of the mouth by a distinct foramen. It anastomoses with the second branch of the glossopharyngeus and innervates the area laterally of that of the r. palatinus. The remainder of the communis component of the facialis usually becomes the r. alveolaris VII, though it may sometimes form a small nerve which I have called "facialis A." The r. alveolaris receives communis fibers from the glossopharyngeus and, in passing along the posterior margin of the suspensorium, lies anteriorly of the pharyngeal evagination which represents the embryonic spiracular cleft. The nerve enters a canal in the mandible and anastomoses, by one division, with the mandibular V. The remainder of the nerve passes out of the canal dorsally of the musculature and is distributed to the epithelium of the floor of the mouth anteriorly. The twig called "facialis A" fuses with the r. pre-trematicus IX. It is possible, and sometimes seems certain, that communis fibers of the facial go to the skin over the suspensorium.

In some instances there are small general cutaneous nerves, which arise more or less independently from the Gasserian ganglion, to the skin over, and caudally of, the exit of the trigeminus from the foramen.

The ganglia of the single glossopharyngeal and the four vagus roots fuse into a ganglionic complex of which the lateralis X ganglion forms the dorsal part; the glossopharyngeal, the antero-ventral part; the general cutaneous X, the postero-ven-

tral part; while the communis X ganglion lies between the lateralis and general cutaneous ganglia. The most anterior and dorsal root of the complex is the lateralis X. Just posteriorly, and considerably below the latter, arises the glossopharyngeal, which is made up of communis and motor fibers. The second root of the vagus is communis and motor; the third, communis, motor and general cutaneous; the fourth, motor.

The t. glossopharyngeus is derived from the entire glossopharyngeal root and from the general cutaneous ganglion of the third vagus root. One division of the general cutaneous component of this nerve passes into the r. jugularis VII, via r. communicans IX + X ad VII. The remainder of this component passes to the skin near the base of the first external gill and of the dorsal surface of the gill itself. The motor component of the nerve innervates the m. levator arcus branchii primi, m. depressor branchii primi and m. ceratohyoideus internus. The communis component forms JACOBSON's anastomosis with the r. palatinus caudalis, connects with the r. alveolaris VII through the r. communicans IX + X ad VII, forms the r. pre-trematicus and r. post-trematicus and pharyngeal rami. A twig of these fibers, also, unites with the r. pre-trematicus of the first truncus branchialis X.

The general cutaneous ganglion of the vagus sends a large component, also, into each of the first two branchial trunks of the vagus. These fibers are distributed to the skin about the base of the second and third gills and to the skin of the upper surface of these gills. The communis component of these two nerves is furnished by the second root of the vagus, as is also their motor component. The former component forms the typical pre- and post-trematic rami, and small pharyngeal rami. The motor component innervates the second and third levator muscles of the gill arches and the muscles of the three external gills, excepting the first depressor branchii. The motor component of the first branchial trunk passes, also, to the m. interbranchiales.

The communis component of the vagus enters, also, the t. visceralis. The fibers entering this trunk are derived from the

third root and perhaps partially from the second root of the vagus. They form a pre-trematic nerve to the third branchial arch, pharyngeal twigs, r. intestinalis, and a r. post-trematicus which is represented in part by a distinct nerve to the distal end of the fourth branchial arch and in part by the r. recurrens vagi. The motor fibers of the t. visceralis come from the fourth root and probably from the third root also. They innervate the m. cucullaris, m. dorso-trachealis, fourth levator arcus, the intrinsic muscles of the glottis, and the m. interbranchiales. The r. supra-temporalis is a purely lateral line nerve which innervates sense organs over the posterior portion of the ear capsule. The r. auricularis vagi is both lateralis and general cutaneous. The lateralis fibers innervate organs located laterally and posteriorly of the territory of the r. supra-temporalis. The remainder of the lateralis component of the vagus forms the r. lateralis superior and r. lateralis inferior which innervate the lateral line organs of the trunk.

The first spinal nerve sometimes has a small ganglion. The second always has a large dorsal root and ganglion. The ventral rami of these two nerves fuse to innervate the m. genio-hyoid and sterno-hyoid. The first nerve innervates the m. basi-scapularis; the second, the m. thoraci-scapularis. The ventral r. of the second carries out, also, a large cutaneous component which is distributed to the skin of the pectoral region. A general cutaneous nerve of the second spinal passes laterad through the musculature to the skin near the base of the third external gill and of the dorsal surface of this gill. It anastomoses with a branch of the second truncus branchialis vagi.

PART SECOND.

A COMPARATIVE DISCUSSION OF THE CRANIAL NERVES OF
AMBLYSTOMA.

I. THE OLFACTORY NERVE.

STIEDA ('75) and HERRICK ('94) consider that the olfactory nerve of *Amblystoma* arises by a single root. Nor do they mention any particular division of the nerve to JACOBSON'S organ. SEYDEL ('95), however, has observed the peculiar branch of the nerve to this organ in larval *Amblystoma*, though he argues that this branching of the olfactory nerve has no morphological significance.

Before criticizing SEYDEL'S conclusion, one should review a few facts concerning the olfactory nerve of Amphibia. In *Gymnophiona* and *Triton* (BURCKHARDT, '91), *Cryptobranchus* (MCGREGOR, '96), *Diemyctylus* (GAGE, '93), and in *Anura* there occurs a greater or less separation of the olfactory nerve into two divisions from the origin of the nerve towards the periphery. In *Gymnophiona* and *Triton* these two divisions are distinct throughout the entire extent of the nerve, and the more ventral of the two innervates JACOBSON'S organ. Also in *Amphiuma* (KINGSLEY, '92) and in *Diemyctylus* (GAGE, '93) and in some other Amphibia there is a particular branch of the nerve, the exact central relation of which is not known, which innervates JACOBSON'S organ. These facts, especially in view of the clear relations in *Gymnophiona* and *Triton*, indicate that there are two morphologically distinct elements in the olfactory nerve of Amphibia.

In the full light, however, of the facts as they appear in *Gymnophiona* and *Triton*, SEYDEL concludes that the particular branch of the nerve which innervates JACOBSON'S organ has no morphological value. He bases this conclusion, largely or wholly, upon the fact that this branch gives fibers, also, to the olfactory epithelium proper. My own observations show that such an interchange of fibers might take place between the two elements of the nerve. However, this fact seems to me of

little importance in consideration of the frequent and striking variation which occurs in the arrangement of the terminal rami of many of the nerves in *Amblystoma*. Furthermore, one should notice that SEYDEL has not observed the division of the proximal portion of the olfactory nerve into two distinct elements. This condition of the proximal end of the nerve is of prime importance, since the neurones from JACOBSON'S organ certainly enter the glomeruli by the postero-ventral element as they do in *Gymnophiona* and *Triton*.

BURCKHARDT considers the ventral (more caudal) root of the olfactory nerve in *Triton* as the homologue of the ventral root of the nerve in *Gymnophiona*. It seem to me certain that this homology can be extended to the postero-ventral element of the olfactory nerve in *Amblystoma*, and possibly to all *Amphibia* which possess the accessory olfactory organ. The anatomical distinctness of the two roots of the nerve may be lost to a greater or less degree, but their morphological significance, on this account, is in no wise less important.

II. THE INNERVATION OF THE EYE MUSCLES.

The work of the earlier anatomists upon the *Amphibia* has left the innervation of the eye-muscles very obscure in some important respects. Even ALLIS ('97) accepts the eye-muscle nerves of *Salamandra* according to SCHWALBE'S ('79, p. 197) observations as typical for the *Urodela*. Yet I have observed no specimen of *Amblystoma* which accords with SCHWALBE'S descriptions. The m. retractor bulbi of *Amblystoma* is not innervated by the oculomotorius as SCHWALBE reports for *Salamandra*; nor is the m. rectus internus innervated by the superior ramus of the third nerve. Either there is great difference in this regard between *Amblystoma* and *Salamandra*, or SCHWALBE has observed an extreme case of variation. However this may be, the eye-muscle nerves of *Salamandra* according to his description can not be accepted as typical of *Urodela*.

HERRICK'S ('99, pp. 391, 392) description of the oculomotor nerve of *Amblystoma* is correct for some individuals, but it will not apply universally. The wide variation in the

eye-muscle nerves, with regard to their exact position relative to the eye-muscles, shows that no type can be established in this particular without a specific study of the variations within the species. And, until such a study has been made, very little morphological significance should be attached to the particular relation which any branch of these nerves may hold to the neighboring parts.

The intimate relation between the trochlearis and a cutaneous branch of the ophthalmicus profundus seems to be present in Amphibia generally. It has led various authors to believe that the ophthalmicus profundus participated in the innervation of the m. obliquus superior. Such a conclusion, however, seems contrary to the condition as it appears in *Amblystoma*.

HERRICK ('94) considers that the m. retractor bulbi is probably innervated by the fifth nerve indirectly through the sixth. I have found no data in favor of this conclusion, unless the observation of fibers passing from the ophthalmicus profundus into the abducens is so interpreted. None of these fibers, however, were traced to the m. retractor bulbi. Moreover, BOWERS' (1900) results speak strongly against HERRICK's conclusion. This author finds a very much greater degree of separation of the sixth from the fifth nerve in *Spelerpes* than there is in *Amblystoma*, and concludes that the m. retractor bulbi is innervated by the sixth. Since the cranial nerves of *Amblystoma* and *Spelerpes* are very similar in other respects, the sixth nerves in the two forms probably have the same distribution. And, since the source of obscurity, the contact with the Gasserian ganglion, is eliminated in *Spelerpes*, BOWERS' conclusions have special significance.

III. THE TRIGEMINAL AND FACIAL NERVES.

In the terminology of the fifth and seventh nerves the earlier students of the cranial nerves of Urodela have been largely followed in this paper, in order to avoid the confusion of implied homologies. "Alveolaris," "mentalis" and "jugularis" are preferable, respectively, to "mandibularis internus,"

"mandibularis externus" and "hyoideus," for example, because our present knowledge does not seem to warrant the application of these latter terms to nerves of Urodela without extensive and precise limitations in each instance. Such limitations would elucidate nothing, and would ultimately tend to confusion.

1.—The Roots and Ganglia.

In his description of the roots and ganglia of the fifth and seventh nerves in *Amblystoma*, STRONG ('95, p. 132) states that the communis VII root arises dorsally of the VIII root. These results differ from mine. In a projection on the sagittal plane the communis VII root is plainly shown to arise dorsally of the ventral VIII but anteriorly (cephalad) of the dorsal VIII root.

KINGSBURY ('95) and BOWERS ('00), also, described the communis VII root as emerging dorsally of the VIII root in *Necturus* and *Spelerpes*. It should be noticed, however, that these two authors do not distinguish two acoustic roots. It is possible that the auditory nerve of *Spelerpes* and *Necturus* differ in this regard from the auditory nerve of *Amblystoma*, but the peripheral relations of the acusticus will scarcely support such an hypothesis. Moreover, STRONG's statement concerning *Amblystoma* suggests that the relative position of the communis root in Urodela has been misinterpreted. Indeed any transverse section of the medulla through the communis root at its origin will show acoustic fibers emerging ventrally of the communis root. But when projected upon the sagittal plane, the auditory fibers are seen to emerge also caudally of the communis root. Excepting the point just mentioned, *Necturus* and *Spelerpes* do not seem to differ from *Amblystoma* with regard to the roots and ganglia of the fifth and seventh nerves. The description of these parts in *Desmognathus* by FISH ('95), however, shows some irregularities. FISH says, "from the common trunk" (evidently referring to the common root of the facial and auditory nerves) "there passes a good sized branch towards the dorsal surface of the Gasserian ganglion." This branch, he maintains, "probably corresponds to the palatinus

branch." Now, the r. palatinus should pass near the ventral surface of the Gasserian ganglion, and any part of the facialis associated with the dorsal surface of this ganglion must be the anterior division of the lateralis VII root.

If this nerve which FISH thus describes is the r. palatinus VII, as his drawings seem to indicate, the lateralis VII root would seem to be absent in adult *Desmognathus*. In the adult of *Amblystoma*, however, there is no apparent diminution of this root or its ganglia. Neither does GAGE ('93) find any reduction of the nerve in adult *Diemyctylus*. In the adult of *Triton*, on the other hand (DRÜNER, '01, p. 573), there is no degeneration of the ganglion of the anterior division of the lateralis VII root, while the ganglion of the posterior division disintegrates upon metamorphosis. Again in the adult of *Salamandra* (DRÜNER, '01, p. 538) both of the lateralis VII ganglia undergo degeneration. In Urodela, therefore, arrested phylogenetic stages may be observed in a process which is complete in the life history of Anura.

So far as the roots and ganglia of the fifth and seventh nerves of Anura are adequately known, their most important differences from those of Urodela are in regard to the relative positions of their ganglia, and in regard to the origin of the communis VII root.

The communis root in *Rana* (STRONG, '95) emerges ventrally of the acoustic root. This separation of the communis VII from the motor VII root is still more marked in *Menidia* and *Gadus* (HERRICK, '99, '00) where the communis root emerges between the lateralis roots. This fact indicates that the difference between Anura and Urodela in this particular cannot be due to correlative changes in the lateralis VII and acoustic roots in *Rana*, as STRONG suggests ('95, p. 114).

The ganglia of the facialis and trigeminus of Anura are fused into a single ganglionic complex while they form two distinct complexes in Urodela. That this difference can be in any way correlated with differences in the peripheral relation of the rami, such as the r. alveolaris and r. mandibularis internus, or with differences in the manner of origin of the communis root

is not probable. Furthermore, Siren (WILDER, '91, p. 677) seems to represent a transition stage in this regard between the typical Urodela and the Anura. WILDER finds the facial (geniculate) ganglion of Siren pushed forward into touch with the Gasserian ganglion. This contact is such that he considers it not improbable that the r. alveolaris receives fibers from the trigeminus. A thorough study of Siren by microscopical methods may throw light upon the fundamental relation of Anura and Urodela with regard to the ganglia in question.

2.—*The Ophthalmicus Profundus and Maxillaris V.*

STRONG ('95, Plate XII, C) has given a reconstruction of the roots and ganglia, and of the proximal portion of the trunks of the fifth and seventh nerves in the *Amblystoma* larva. With regard to the rami issuing from the Gasserian ganglion and the ganglion of the anterior division of the lateralis VII root, this reconstruction is certainly incorrect. The absence of reference latters, also, leaves doubt as to the author's interpretation of his figure. He represents here two lateralis VII rami which leave their ganglion in union with general cutaneous components from the Gasserian ganglion. In addition to these two rami, he figures a third purely lateralis nerve. Now, the only pure lateralis nerve which goes out of this ganglion is the r. ophthalmicus superficialis VII; while the only nerve in this region which is composed of lateralis and general cutaneous fibers is the t. infra-orbitalis. The second nerve figured by STRONG as composed of lateralis and general cutaneous fibers is not found in *Amblystoma*.

In an earlier communication (1901) I have discussed the relation of the r. ophthalmicus profundus and r. maxillaris of *Amblystoma* to the nerves of the same name in *Anura*. The essential results and argument of that communication may be summarized as follows:

1. The r. maxillaris V of *Rana* is represented in *Amblystoma* by a part of the r. ophthalmicus profundus.
2. The r. maxillaris V in *Amblystoma*, by which is meant the general cutaneous nerve more or less fused with the

r. buccalis VII, is not the homologue of the r. maxillaris of Rana, but is homologous with the nerve described by STRONG as an "accessory" branch of the trigeminus in the tadpole.

3. The terminal branches of the r. ophthalmicus profundus in Amblystoma are not homologous with the terminal branches of that nerve in Rana.

In support of the first conclusion I have shown (a) that a branch from the r. ophthalmicus profundus in Amblystoma anastomoses in the roof of the mouth with a palatine VII branch which is homologous with a nerve fusing with a branch of the maxillaris V in Rana; (b) that corresponding cutaneous areas are innervated by a part of the r. ophthalmicus profundus in Amblystoma and by the maxillaris V in Rana.

As to my second conclusion, I have shown that the two nerves under consideration correspond in striking detail (a) with reference to their relation to the Gasserian ganglion, (b) in their relation to the r. buccalis VII, and (c) in their peripheral distribution.

The extent of the fusion of the "accessory" ramus with the r. buccalis VII is reduced to a minimum in the tadpole while in Amblystoma the extent of the corresponding fusion varies greatly. It may take place immediately outside the ganglion and continue to the region of the eye; or the two components may not meet until they reach the lateral border of the temporalis muscle. In young Spelerpes, according to BOWERS, the two components of this nerve may be distinct throughout their entire extent; and PLATT's studies ('96, p. 520) show that the same condition may occur in young Necturus. These observations of BOWERS and PLATT indicate that Necturus and Spelerpes, in this particular, hold an intermediate position between the tadpole and Amblystoma, and afford important evidence in favor of my conclusion concerning the homology of the r. maxillaris V in Amphibia. The question may become elucidated further by an adequate study of certain irregularities which appear in the arrangement of the trigeminal rami in Cryptobranchus (FISCHER, '64; WILDER, '92; MCGREGOR, '96), Amphiuma and Siren (WILDER, '91, '92), and in

Caecilians (WALDSCHMIDT, '87). In these forms certain twigs of the r. maxillaris seem to fuse with twigs of the r. ophthalmicus profundus; but it is impossible to interpret this condition until the composition of these twigs is known. In none of these forms have the observers differentiated the lateralis from the general cutaneous fibers.

HERRICK ('99) describes, in *Menidia*, a nerve ("10, 2") which is given off from the truncus infra-orbitalis at the posterior level of the eye, and the general cutaneous part of which he says "corresponds in nature and position rather closely to the most lateral one of the accessory trigeminal branches in the tadpole of the frog." Also, in *Amia* (ALLIS, '97, p. 605), in *Chimaera* (COLE, '96, p. 649) and in *Gadus* (COLE, '98, p. 159; HERRICK, 1900, p. 280), homologues of one or more of the "accessory" rami of the trigeminus in the tadpole have been recognized. These proposed homologies introduce a question concerning the morphology of these accessory nerves which was not discussed in my earlier communication: i. e. if the so-called r. maxillaris of *Amblystoma* is not homologous with that of *Rana*, which of these nerves represents the r. maxillaris of fishes?

If the "accessory" ramus of the tadpole is represented in fishes by small branches of the t. infra-orbitalis as ALLIS, COLE and HERRICK maintain, and if it is represented in the *Amblystoma* by the entire general cutaneous component of the infra-orbital trunk, then there can be no r. maxillaris of the piscine type in *Amblystoma*. On this hypothesis, also the r. maxillaris of fishes would become the equivalent of the r. maxillaris of *Rana*. However, though my conclusions concerning the amphibian nerves may introduce new questions of interpretation, they do not seem to me to increase the difficulties. On the other hand, they seem to elucidate the main question at issue, which is to explain the differences in the so-called r. maxillaris as it appears in the three types, *Urodela*, *Anura* and fishes.

In the consideration of this question one well known fact should be emphasized: the r. maxillaris of *Rana* is anatomically

distinct from the r. buccalis VII, while the r. maxillaris of fishes is fused with the r. buccalis VII for a long distance. Moreover, the so-called r. maxillaris of *Amblystoma* corresponds in a striking manner with the r. maxillaris of fishes in this important feature. Furthermore, the rr. mandibularis, maxillaris and buccalis of *Amblystoma* are sometimes fused for a considerable distance into a typical piscine t. infra-orbitalis.

The relation of the r. maxillaris to the r. palatinus VII, also, should be noticed especially. I have pointed out that the r. maxillaris of *Amblystoma* differs from that of *Rana* in this relation. Whether the r. maxillaris of fishes corresponds with that of *Amblystoma* in this particular cannot be stated certainly, excepting for a few forms. In *Gadus* and *Menidia*, two fishes which have been most thoroughly studied from the point of view of nerve components, there is not any contact between the r. maxillaris V and r. palatinus VII (HERRICK). ALLIS has described an anastomosis between these nerves, however, in *Amia*. Such an anastomosis has been described also in *Silurus* (see HERRICK, 1901, p. 199). However, according to our knowledge of these two anastomoses, they may take place through communis fibers of the r. maxillaris. If they are of such a nature, they have no bearing upon the present discussion, since the anastomoses in *Amphibia* take place through the general cutaneous component of the trigeminus. There is no satisfactory evidence, therefore, that the r. maxillaris of fishes ever agrees with that of *Anura* in its relation to the r. palatinus VII.

In the light of these facts concerning the r. maxillaris and "accessory" rami in fishes, *Urodela* and *Anura*, I am inclined to think that the so-called maxillaris of *Amblystoma* and the "accessory" ramus of the tadpole are the morphological representatives of the r. maxillaris of fishes functionally very much reduced, and that the r. maxillaris of the tadpole is an essentially different nerve. This conclusion, however, is only tentative, pending a thorough study of other *Amphibia*, such as *Amphiuma*, *Siren* and *Gymnophiona* from this point of view.

My third conclusion, concerning the terminal rami of the

r. ophthalmicus profundus V in Amblystoma and the tadpole, follows from the conclusions already discussed. The lateral and mesial terminal branches of this nerve in Amblystoma innervate an area which corresponds very closely to that innervated in Rana by the medialis and lateralis narium of GAUPP ('97) and the r. maxillaris. Within this area in Amblystoma the variation of the manner of branching is so great that it is impossible to establish any positive relation between the two forms in this particular. It seems reasonable that the communicating nerves of the general cutaneous component of the trigeminus to the r. palatinus VII in Anura have their equivalents in the two divisions of the ventral terminal branches of the r. ophthalmicus profundus in Amblystoma. The divergence of Amblystoma and Rana in this portion of the peripheral nervous system is much greater, I believe, than has been generally accredited; and the application of anuran terminology to the nerves of Urodela, as BOWERS has applied it to Spelerpes, is not only incorrect in this case but tends to obscure the actual condition of relationship.

3.—*Minor Branches of the Trigeminus.*

The second and third branches of the r. ophthalmicus profundus in Amblystoma seem to be represented in Spelerpes by a single nerve which is called "*Va*" by BOWERS. The first cutaneous branch of the r. mandibularis V of Amblystoma, also, is represented in Spelerpes by a nerve which BOWERS figures as "*Vd*." The latter nerve is probably represented in Cryptobranchus by the nerve which MCGREGOR describes as penetrating the m. masseter and running "latero-caudad," supplying the skin over the muscle mentioned and about the angle of the jaw. MCGREGOR says this nerve "may represent STRONG's ramus accessorius." Such a relation, however, seems wholly improbable, as shown by the above discussion of the latter nerve.

The anastomosis between the r. mandibularis V and the r. alveolaris VII is not found by BOWERS in Spelerpes. This relation will be noticed particularly in connection with the r.

alveolaris VII. In *Spelerpes*, also, the second and third cutaneous branches of the mandibularis V of *Amblystoma* are represented by a single nerve.

The two accessory trigeminal twigs which I have described as occurring sometimes in *Amblystoma* seem not to have been noticed in other Urodela. They may correspond in an indefinite manner to the two inner "accessory" trigeminal rami of the tadpole as described by STRONG; but they are so variable in their occurrence that their morphological value cannot be determined without microscopical study of a large series of specimens.

4.—*The Lateralis Component of the Facialis.*

The t. hyomandibularis proper scarcely extends beyond the lateral border of the ear capsule in *Amblystoma*. It agrees in this regard with the same trunk in *Spelerpes* (BOWERS), *Salamandra*, *Triton*, *Necturus* and *Proteus* (DRÜNER, '01). In *Anura* the trunk extends to the region of the angle of the jaw as it does in many fishes. The composition of this trunk in all *Amphibia*, so far as they have been adequately studied, is *lateralis*, *motor* and *communis*. In no case have any of its neurones been found to enter the *tractus spinalis n. trigemini*. The assignment of a general cutaneous function to certain of its rami will be noticed in a following paragraph.

The nomenclature of the *lateralis* component of this trunk in *Amphibia* is unfortunately mixed. I have employed the "mentalis" of earlier authors to include the entire *lateralis* component of the trunk. Excepting the erroneous application of this term to the r. mandibularis internus of *Anura* by certain earlier authors (HOFFMANN, '78), "mentalis" has been most used in the anatomy of Urodela. In treating *Spelerpes* BOWERS has used STRONG's terminology for the tadpole, "mandibularis externus," without limitations. This usage is probably in a general way correct, in the light of KINGSBURY'S ('95) work on the lateral line system of *Amphibia*. But owing to important differences in regard to the other rami of the hyomandibular trunk of Urodela on the one hand and *Anura*

on the other, it seems best for the present to retain the entire system of terminology which is more typically urodelian.

DRÜNER, in his late work on Urodela, considers that the lateralis component of this trunk is divided from the ganglion into two distinct nerves which he calls "R. cutaneus mandibularis lateralis" and "R. cutaneus mandibularis medialis." These rami, which he describes in *Salamandra*, *Triton*, *Menobanchus* and *Proteus*, are equivalent respectively to my r. mentalis externus and r. mentalis internus. However, because of the confusion of the terms "cutaneus" and "lateralis," DRÜNER's terminology cannot be conveniently used in treating of the components of the nerves.

The distribution of the r. mentalis seems to be very constant in those Urodela which have been studied. The topography of the head of Anura, however, is so modified and different from that of Urodela that it becomes very difficult to make any useful comparisons of the nerve in the two types from a study of advanced larvae alone. Owing to the great number of lateral line sense organs, to their variableness and to their transitory character in the larval stages, the first embryonic appearance of individual organs and their process of grouping must be studied exhaustively in a number of types before valuable contributions can be made to the morphology of these lateral line nerves of Amphibia.

5.—*The Branchial Rami of the T. Hyomandibularis.*

The other two components of this trunk, the motor and communis neurones, form the rr. jugularis and alveolaris in Urodela, the rr. hyoideus and mandibularis internus of Anura. These nerves are all interpreted by most authors as branchial nerves. The exact relation which they severally hold to the branchial clefts is of special interest.

With regard to the branchial value of these rami in *Necturus*, PLATT ('96, p. 534) says: "The true post-trematic nerve of the hyoid arch is the hyomandibularis and its ventral continuation, the 'internal mandibular.' Nor do I regard the external mandibular nerve as the pre-trematic nerve of the

group, but because of its relation to the mouth would homologize it also with the post-trematic nerves." Elsewhere in the same contribution it is stated that "the inner row of mandibular sense organs at the margin of the lower lip is innervated by the hyomandibularis (mandibularis internus)." PLATT, therefore, considers the r. mandibularis internus as a post-trematic nerve innervating lateral line sense organs. This author believes that these organs are in part innervated by the general cutaneous system; but the r. mandibularis internus is not even general cutaneous but communis in function. Moreover, lateral line nerves cannot be classed in the branchial system as STRONG, HERRICK and others have conclusively established. The nerve which PLATT has thus interpreted in *Necturus* as the mandibularis internus is in all probability the mentalis internus according to DRÜNER's report upon *Menobranchius*, and on account of its function should be distinguished sharply from the branchial rami of the hyomandibular trunk.

STRONG interprets the r. mandibularis of fishes, and of *Anura*, the r. alveolaris of *Urodela* and the mammalian chorda tympani as homologous structures. BOWERS adopts STRONG's interpretation for *Spelerpes*. COLE ('96, p. 660) considers the r. mandibularis of *Anura* as a pre-trematic nerve fused with the post-trematic, an hypothesis based upon his view that the typical post-trematic nerve is motor only. DRÜNER looks upon the r. alveolaris as a pre-spiracular nerve but denies that it is the homologue of the chorda tympani, since he accepts FRORIEP's idea that the chorda tympani is a post-spiracular nerve. DRÜNER claims, further, that the r. jugularis cannot be considered as belonging to the post-trematic VII. These conflicting opinions of recent authors show that the morphology of the branchial rami of the facialis in *Amphibia* is in a most unsatisfactory state. It is the purpose of the following paragraphs to emphasize a number of important facts which have not been properly recognized in their bearing upon this question.

My interpretation of these rami may be stated as follows:

1. The r. alveolaris VII is a pre-spiracular nerve and as

such cannot be the homologue of the r. mandibularis internus of Anura and fishes. It represents a communis pre-spiracular branch of the facialis in Selachia, which is shown with special clearness in *Squalis acanthias* (GREEN, '00, Fig. 1, p. 416). It is probably the true representative of the chorda tympani in the Ichthyopsida.

2. The r. mandibularis internus of Anura is a post-spiracular nerve and is not represented by any nerve in Urodela, excepting possibly by a small nerve to the r. pre-trematicus IX.

There is a difference which appears superficially between the r. alveolaris and the r. mandibularis internus in regard to their manner of origin from the t. hyomandibularis. This difference has been explained by several authors as due to the difference in the topography of the head of the two forms. It may be of more significance than this. Not only does the r. alveolaris arise much nearer than does the r. mandibularis internus to the geniculate ganglion, but there are certain anatomical modifications of the cranium in some species which must be significant. In *Proteus* and *Menobranthus*, for example, DRÜNER (591, 607) describes the hyomandibular trunk as passing out of the cranium in two divisions in such a manner that the r. jugularis becomes separated from the r. alveolaris by an osseous projection of the cranium which unites by syndesmosis with a similar projection of the suspensorium. Moreover, a still greater modification appears in *Siren*. In this Urodele WILDER ('91) describes the r. alveolaris as passing out of the cranium in union with the r. palatinus. Such a difference as this from the usual arrangement in Urodela certainly cannot be explained on the basis of topographical modification of the head. On the contrary, it seems to indicate that the r. alveolaris of Urodela occupies a position which is morphologically anterior of the r. mandibularis internus.

Other data, also, lead to the same conclusion. The r. mandibularis internus, in fishes, as a part of the t. hyomandibularis, passes to the lower jaw posteriorly of the spiracular cleft. In Anura it holds the same position with reference to the tympanum and Eustachean tube. Now, the Eustachean

tube in *Rana* and *Bufo* has been traced by SPEMANN ('98) and (FOX) ('01) in its ontogenesis from the embryonic spiracular cleft. This nerve, therefore, is post-spiracular. On the other hand, the r. alveolaris in larvae of *Amblystoma*, in reaching the lower jaw, passes anteriorly (cephalad) of the deep pharyngeal evagination which represents the embryonic spiracular cleft. Furthermore, having reached the lower jaw, the r. mandibularis internus still lies morphologically behind the position of the r. alveolaris. In young larvae of *Amblystoma* the r. alveolaris lies dorsally of the m. mylo-hyoideus, a position which the nerve always holds in *Proteus* and *Menobranchius* (DRÜNER). In older larvae and in the adult of most *Urodela* the nerve becomes enveloped in a canal by the ossification of the mandible and its relative position to the muscles may become somewhat changed here, but when it emerges from the canal it emerges dorsally of the musculature. In *Anura*, on the contrary, as GAUPP ('97) clearly states, the r. mandibularis internus lies ventrally of the m. mylo-hyoideus and sends its fibers through this muscle to innervate the oral epithelium. This is essentially the relation of the r. mandibularis internus of fishes, also.

Still other important differences between these amphibian nerves should be emphasized. In *Amblystoma* the r. alveolaris receives fibers from the glossopharyngeus and anastomosis with the trigeminus. These relations do not occur universally in *Urodela*, but the latter anastomosis is frequent and perhaps universal. In none of these features does the r. alveolaris agree with the r. mandibularis internus.

In spite of these striking differences, however, the nerves in question have two important features in common, area of distribution and central termination. These are two of the criteria of homology in nerves and they must be kept in mind in considering the third criterion, the relation of the nerves to other important structures. An explanation, therefore, which is offered for the differences between the nerves must explain also their features of perfect resemblance.

Such an explanation as I have indicated is found by a com-

parison of Amphibia with certain Selachia. In these fishes, as STANNIUS ('49) and HERRICK ('99, p. 321) point out, there is a post-spiracular r. mandibularis internus and a communis pre-spiracular nerve which agrees in a striking manner with the r. alveolaris of Urodela. This pre-spiracular nerve is shown nicely in *Squalus acanthias* by GREEN's dissections ('00, p. 416). It should be noticed that these two nerves in *Squalus*, the r. mandibularis internus and the "chorda tympani" of GREEN, innervate areas which in part coincide and that the terminal fibers of the two nerves anastomose. Here, then, are post-trematic and pre-trematic neurones which have a common central termination and a common area of distribution. Now, if we assume that the amphibian facialis, in its phylogenetic development, has passed through a condition similar to this found in *Squalus*, the two amphibian types of the nerve may have arisen by a very simple process of divergence from this hypothetical ancestral type. Upon this hypothesis, specialization of the ancestral pre-spiracular nerve with degeneration of the post-spiracular in the Urodelian line, and specialization of the post-trematic with degeneration of the pre-spiracular in the anuran line, would account for the r. mandibularis internus and the r. alveolaris with their respective peculiarities without violation of any of the criteria of homology.

On the above hypothesis, also, such a condition as that described by WILDER for *Siren lacertina*, where the r. alveolaris arises from the r. palatinus (WILDER's palatinus anterior), becomes perfectly intelligible. Indeed, this condition is very like that found in *Squalus*. From this point of view, again, the r. alveolaris and the r. mandibularis internus would not be expected to agree in their relation to the glossopharyngeus and trigeminus. This explanation of the conditions, I believe, is adequate and in accord with the facts.

With regard to the relation of these amphibian nerves to the mammalian chorda tympani, it must be admitted that there is a wide gap between the Amphibia and any mammal the cranial nerves of which have been adequately studied for purposes of comparison from the point of view of nerve compo-

nents. A comparison between these nerves should await thorough embryological studies of the nervous system of the lowest Mammalia. Any position taken at present upon the point must be only tentative. It seems certain, however, that the chorda tympani should be considered as passing morphologically in front of the Eustachean tube and tympanum (HERRICK, '99, p. 316) and that it should therefore be considered as a pre-spiracular nerve. This being true, its most complete morphological and physiological representative in the Ichthyopsida is probably found in the r. alveolaris of Urodela.

There are certain variations in the course of the r. alveolaris in Urodela which are of doubtful significance. In *Amblystoma*, *Salamandra* (DRÜNER, p. 493) and *Triton* (DRÜNER, p. 562) the nerve enters a canal between MECKEL'S cartilage and the bones of the mandible. FISCHER ('64) finds such a canal in *Siren*, but WILDER ('91) denies its existence. In *Proteus* and *Menobrachius* (DRÜNER, pp. 592, 608) the nerve passes cephalad dorsally of the musculature and mesially of the mandible. BOWERS, also, reports such a condition in *Spelerpes*. The presence, also, of the anastomosis with the trigeminus in the lower jaw is doubtful for some Urodela. It does not seem to occur in *Proteus* and *Menobrachius*, according to DRÜNER'S descriptions and is lacking in *Spelerpes* (BOWERS).

DRÜNER'S position with regard to the r. jugularis is best stated in his own words (p. 449): "Der R. jugularis der Urodelen trägt keine Kennzeichen, dass in seinem Facialsantheil der R. posttrematicus VII zu suchen ist. An der Stelle am Knorpel des Hyoidbogens, wo man einen solchen vermuthen könnte, fehlt ein Nerv—ebenso wie eine Kiemenbogenarterie daneben. Sensible oder sensorische Nerven des Facialis für den ventralen Theil der Schleimhaut der Mundhöhle verlaufen zwischen I. Schlundspaltentasche und I. Kiemenspalte nicht."

Judging, however, by the function, central origin and relation to the gill clefts, it is obvious that the r. jugularis and r. hyoideus of the *Anura* are morphologically equivalent structures. The fact, also, that they both receive the communicating nerve from the vagus is additional proof that they have a

common origin phylogenetically. And when the *r. hyoideus* of *Anura* is compared with that of fishes there can be little ground for denying their equivalence. From this point of view the *r. jugularis* must be morphologically a branchial nerve and essentially post-trematic.

The innervation of the *m. cerato-hyoideus externus* should be noticed also in connection with the *r. jugularis*. The variation in the innervation of this muscle within the *Urodela* is remarkable unless there have been numerous errors in observation. In *Amblystoma* the muscle is innervated by the *r. jugularis* VII, though FISCHER states that it gets fibers also from the *t. glossopharyngeus*; in *Cryptobranchus japonicus* (HOFFMANN) by the *r. jugularis* and *glossopharyngeus*; in *Cryptobranchus alleghaniensis*, by the *glossopharyngeus*; in *Salamandra* according to HOFFMANN by the *r. jugularis* and *glossopharyngeus*, according to DRÜNER by the *r. jugularis* and *r. communicans*; in *Triton*, *Menobranchus* and *Proteus* by the *r. jugularis* and *r. communicans* (DRÜNER); in *Siren* according to HOFFMANN by the *glossopharyngeus*, according to WILDER by the *glossopharyngeus* and posterior palatine; in *Amphiuma* (HOFFMANN) by the *glossopharyngeus*; in *Spelerpes* by the *glossopharyngeus* (BOWERS).

A study of these observations will show that in all cases where the *glossopharyngeus* is reported to take part in the innervation of the *m. cerato-hyoideus externus*, the methods of investigation were largely or wholly dissection, excepting in the investigations by DRÜNER and BOWERS. And in no case does DRÜNER describe fibers from the *glossopharyngeus* to this muscle excepting through the *r. communicans*, which he erroneously interprets as motor. Now, the *t. glossopharyngeus* passes between the *m. cerato-hyoideus* at or near its insertion and the branchial cartilage in a manner which might lead a dissector to believe that it gives fibers to this muscle, but serial sections show that, in every case of my observation, the nerve passes through this relation intact. DRÜNER, also, notices this fact in the *Urodela* which he studied. But for BOWERS' observation upon *Spelerpes*, the above facts would lead one to think

that the m. cerato-hyoideus externus of Urodela is probably always innervated by the n. facialis. And considering the age of the specimens upon which BOWERS reported, it is not improbable that this apparent exception may not hold on further examination, and that this muscle will prove to lie wholly within the territory of the facial nerve.

6.—*The Rami Palatini*.

In my discussion of the r. maxillaris V, I have mentioned the important features in which the r. palatinus of *Amblystoma* corresponds with that of *Rana*. These nerves were discussed, also, in my communication upon "The Rami of the Fifth Nerve of Amphibia," where it was shown that they correspond closely in the arrangement of their terminal rami with reference to the internal nares. The branching posteriorly of the internal nares takes place relatively earlier in *Rana* than in *Amblystoma*, but in both cases each division anastomoses with a general cutaneous trigeminal nerve. The lateral branches in the two forms innervate morphologically equivalent areas. The same is true of the mesial branches. This relation has not been observed in other Urodela but it is probably typical for both *Anura* and Urodela.

The r. palatinus caudalis was described by HERRICK ('94) in *A. punctatum* under the same name. A corresponding nerve in *Necturus* is described by PLATT ('96, p. 532); and it occurs also in *Spelerpes* (BOWERS). DRÜNER (p. 561) reports a similar nerve in *Triton*, which he considers as a part of the r. palatinus proper. He does not report it in *Proteus*, *Menobranchus* and *Salamandra*.

The nerve which WILDER calls posterior palatine in *Siren* is of doubtful significance. The peculiar relations of the communis component of the facial nerve in *Siren*, by which the r. alveolaris comes to arise from the r. palatinus and the posterior palatine from the r. alveolaris, obscures the true nature of all these nerves. This obscurity is further increased by WILDER's statement that the posterior palatine gives motor fibers to the m. cerato-hyoideus externus. The nerve seems to pass more

caudad than the r. alveolaris; also. There are important differences, therefore, between the posterior palatine of Siren and the palatinus caudalis of Amblystoma, and it may be that they are not homologous.

IV. THE GLOSSOPHARYNGEUS AND VAGUS.

1.—The Roots.

The origin of the glossopharyngeus by a single root and of the vagus by three major roots, exclusive of the lateralis root, seems to be a constant arrangement in Amblystoma. In essential matters, the presence of communis and motor fibers in the glossopharyngeal root, and of communis, motor and general cutaneous fibers in the vagus roots, in addition to a distinct lateralis root, Amblystoma agrees with Rana (STRONG), Necturus (KINGSBURY) and Spelerpes (BOWERS).

KINGSBURY ('95) doubts the relation of the most posterior root of the vagus to the eleventh nerve of higher vertebrates, and considers that it is partly general cutaneous in Necturus. DRÜNER considers that the root is related to the trapezius muscle, but does not trace it through the ganglia in the Urodela which he investigated (Salamandra, Triton, Menobranchus and Proteus). In Amblystoma, however, the manner of origin and the distribution of the nerve afford strong evidence that it is to be considered as the true representative of the n. accessorius.

In his work upon Urodela DRÜNER treats the lateralis and glossopharyngeal roots as a single root, but recognizes the functional value of the two parts. His observations, on the whole, indicate that the relations of the roots of this complex in the Urodela he studied agree in all essential features with those of Amblystoma.

KINGSBURY has given a detailed account of the smaller divisions of these roots as they emerge from the brain in Necturus. The variation, however, either developmental or individual, is so great in Amblystoma that little emphasis can at present be placed upon any particular arrangement of these minor rootlets of the ninth and tenth nerves. They have no

constant arrangement which can be compared with that of *Necturus*.

2.—*The Lateral Line Component.*

The *r. supratemporalis* of *Amblystoma* corresponds to the nerve of that name described by STRONG for the tadpole of the frog. Here as in *Amblystoma* it arises as a distinct nerve from the ganglion and is a purely lateral line nerve. The nerve which BOWERS calls *R. supratemporalis* in *Spelerpes* arises from the ganglion in union with the *r. auricularis* and separates from the latter soon after leaving the ganglion. This nerve, according to BOWERS' descriptions and figures, cannot represent the *r. supratemporalis* of *Amblystoma*, but is a part of the *r. auricularis* which is both *lateralis* and *general cutaneous*.

According to DRÜNER's researches, the *r. supratemporalis* is probably absent in *Triton*, *Salamandra* and *Proteus*. In *Menobranchus*, however, this author describes a small nerve which arises independently from the ganglion and sends fibers to the skin. He describes it, also, as innervating the first *m. levator arcus branchii* (p. 609). This nerve, I believe, is the *r. supratemporalis*. As described in Part First of this paper, one division of this nerve may penetrate the *m. levator arcus branchii*. There is no evidence, however, of any of its fibers terminating in the muscle. Moreover, the nerve is derived from the *lateralis* root, which contains no motor fibers. In failing to trace this small division of the nerve through the muscle, no doubt, DRÜNER has been led to interpret it as motor.

The *r. auricularis vagi* of *Amblystoma* is in part a lateral line nerve. In the tadpole (STRONG) and in *Spelerpes* (BOWERS) it is purely *general cutaneous*. However, as suggested in the above paragraph, the nerve which BOWERS interprets as lateral line in function is in all probability a branch of the *r. auricularis*. This entire nerve appears essentially in the same relations in *Salamandra*, *Triton*, *Proteus* and *Menobranchus*, and DRÜNER recognizes in these forms also that it contains fibers to the lateral line sense organs. It seems certain, therefore, that

the r. auricularis of Urodela is typically a general cutaneous and lateralis nerve, and that it differs in this respect from the r. auricularis of Anura.

The rr. laterales superior and inferior of Urodela, so far as they have been investigated, seem to agree perfectly with those of Amblystoma. One apparent exception to this arrangement, however, occurs in Spelerpes. In this species, BOWERS ('00, Figs. 1, 2, *mm. Scap?*) describes a nerve which agrees in origin and position with the r. lateralis inferior of other authors, but represents it as a motor nerve (p. 191). As pointed out in Part First, this nerve in Amblystoma sometimes assumes intricate relations with the brachial nerves and penetrates muscles in such a manner that its course becomes obscure, but its relations are usually perfectly clear. There can be no doubt of its lateralis nature in other Urodela, and it is extremely improbable that its exact position should be assumed by a motor nerve in Spelerpes.

3.—*The R. Communicans IX+X ad VII.*

This branch of the t. glossopharyngeus was treated by earlier anatomists as belonging to the ninth nerve. STRONG maintains that the nerve in anurous larvae is general cutaneous and therefore belongs to the vagus, there being no such component in the glossopharyngeal root. BOWERS figures the nerve as general cutaneous in Spelerpes, but retains the name "r. communicans IX ad VII."

DRÜNER, in his recent work on Urodela, treats this nerve as purely motor in function. My studies of Amblystoma, however, show conclusively that the nerve contains general cutaneous fibers from the vagus and communis fibers from the glossopharyngeus. The general cutaneous fibers I have interpreted as entering the r. jugularis and the communis fibers, as entering the r. alveolaris. The passage of the communis fibers into the r. alveolaris has not been noticed in other Urodela, though FISCHER ('64) probably observed it in Siredon since he mentions a band of fibers which passes from the r. jugularis

into the r. alveolaris after the former nerve has been joined by the r. communicans.

According to HOFFMANN ('78) this r. communicans is absent in *Proteus* and *Menobrachius*, and according to PLATT, also, it is wanting in *Necturus*. DRÜNER, on the contrary, finds the nerve in a reduced condition in both these forms. It is probable, therefore, that the nerve occurs in all *Urodela*.

DRÜNER's idea concerning the function of the r. communicans deserves special attention here. He says (p. 496): "So scheint es, als ob die vom R. jugularis versorgte Musculatur in allen Theilen von Glossopharyngeus-Elementen durchsetzt ist." This relation, he believes, is brought about through the r. communicans.

Now it is very plain in serial sections that many of the terminal ramuli of the r. jugularis contain both motor and general cutaneous fibers. Moreover, DRÜNER's method of dissection does not seem to me adequate to determine the exact nature of these terminal ramuli as they appear in serial sections. Furthermore, he has obviously been deceived concerning the function of a part of the r. supratemporalis which is very like these ramuli in its relation to the muscles and skin.

A most important objection to DRÜNER's interpretation is that it does not account for the presence of the general cutaneous fibers which are known to be in the r. jugularis. Such fibers cannot come from the t. hyomandibularis in *Amblystoma*, nor in any other amphibian which has been studied from the point of view of nerve components. Moreover, general cutaneous neurones from the third vagus root enter the r. communicans in *Amblystoma*. Neurones, also, enter it from the glossopharyngeus which appear to be communis. Therefore, if there is a motor component in this nerve in addition to these two known components, that component must be extremely small and can scarcely have such an important function as DRÜNER assigns to it.

DRÜNER's statement (p. 540) that fibers sometimes pass from the r. communicans directly to the m. cephalo-dorso-mandibularis (depressor mandibulae) is also open to some ques-

tion. There are sometimes fibers to this muscle in *Amblystoma* which superficially appear to come from the r. communicans but which in serial sections plainly come from the r. jugularis.

In view, therefore, of the sensory nature of this nerve in *Anura* (STRONG) and in view of the strong evidence which *Amblystoma* affords of its sensory nature in *Urodela* also, DRÜNER's interpretation should be received with a considerable degree of caution.

4.—*Jacobson's Anastomosis.*

JACOBSON's anastomosis does not occur in *Anura*, and is not found in some *Urodela*. BOWERS does not find it in *Spelerpes*. DRÜNER observes nothing akin to it in *Salamandra*, but finds fusions of branches of the facialis and glossopharyngeus to the pharyngeal epithelium in *Triton*, *Proteus* and *Menobranhus*. In *Triton* (p. 573) the fusion takes place with the major division of the r. palatinus; in *Proteus* (p. 591), by a plexus formed with the most caudal branches of the r. palatinus; in *Menobranhus*, between pharyngeal twigs which are not fully defined.

The anastomosis in *Amblystoma* is of variable strength, and twigs from the glossopharyngeal nerve may fuse with twigs from the r. palatinus proper. However, the usual strength of the anastomosis indicates that it is typical for *Amblystoma*. The fusion of twigs from the glossopharyngeal branch to the anastomosis with twigs from the r. palatinus may be accidental, or they may indicate a tendency towards disintegration of the typical anastomosis into a diffuse plexus such as DRÜNER describes for *Proteus* and *Menobranhus*.

This anastomosis as it appears in *Amblystoma* may have important bearing upon the question which HERRICK and COLE (HERRICK, '01, p. 194) have raised concerning the anastomosis of the same name in fishes. As the latter anastomosis is described by HERRICK and COLE for the cod fish it appears, superficially, to be identical with that of *Amblystoma*. However, in view of COLE's view concerning the branchiomic position of the pseudobranch, HERRICK ('01, p. 195) says, "if

the teleostean pseudobranch proves to be.....a hyoidean demibranch, rather than mandibular, then the posterior palatine must be the post-trematic branch of the facialis, if it is a branchial nerve at all." In the same discussion COLE proposes that the JACOBSON'S anastomosis in teleosts is the pre-trematic IX with fibers from the facialis (posterior palatine).

Now, if the so-called JACOBSON'S anastomosis of Amblystoma represents that of fishes, how can we account for the r. pre-trematicus IX which appears in Urodela in addition to the glossopharyngeal branch to the anastomosis? It is possible that my second branch of the t. glossopharyngeus, which forms the anastomosis with the r. palatinus caudalis, represents a part of the r. pre-trematicus, since the latter nerve sometimes arises in part from the second branch. Again, there is sometimes in Amblystoma, and also in Triton (DRÜNER), a small branch of the facialis which anastomoses with the r. pre-trematicus IX. This anastomosis in reality corresponds more closely with JACOBSON'S anastomosis of teleosts, if COLE is correct in his view that the glossopharyngeal branch concerned in teleosts is pre-trematic. Furthermore, the nerve resulting from the JACOBSON'S anastomosis of Urodela passes far cephalad in the roof of the mouth while the r. pre-trematicus IX holds a typical position in the hyoid arch.

HERRICK believes that the glossopharyngeal branch to the anastomosis in the cod fish is the palatine branch of the nerve. This, I believe, is the case in Amblystoma, since the nerve gives off numerous twigs to the pharyngeal epithelium. However, it cannot be affirmed that the so-called JACOBSON'S anastomoses of Urodela and fishes are homologous structures until their relations are better understood in both forms.

5.—*Rami Pre-trematici*.

A statement made by PLATT ('96, pp. 532,3) concerning a "pre-trematic" nerve in Necturus is open to some question. This writer says: "The lateral branchial nerve, which, as in the younger embryo, extends backwards and outwards, now fuses with a pre-trematic branch from the first vagus nerve.

This is the only pre-trematic branch as yet found in *Necturus*. The two nerves after their fusion supply the lateral musculature, the vascular system, and the skin, including the external gill."

The statement that this nerve which is called "pre-trematic" participates in the innervation of the external gill and the muscles shows conclusively that it is not a pre-trematic nerve in the strict sense. It is, without doubt, my fifth branch of the first t. branchialis X, which has nothing to do with the gill arches or the gill clefts, and on that account cannot be ranked as either a pre-trematic or a post-trematic nerve. The fact, also, that DRÜNER finds a typical pre-trematic branch of the first branchial X trunk in *Menobrachius* is additional evidence against PLATT's interpretation of this nerve.

The series of pre-trematic rami of the glossopharyngeus and vagus which I have described for *Amblystoma* has been found by DRÜNER, also, in *Salamandra* and *Triton*. The first two nerves of the series have been observed, also, by DRÜNER in *Proteus* and *Menobrachius*. It seems certain, therefore, that these nerves are typical for Urodela. Furthermore, they seem to be strictly homologous with the pre-trematic nerves of fishes, and their discovery proves a closer relationship between the branchial innervation in fishes and Amphibia than was formerly recognized.

The anastomoses which I have described between the pre-trematic and post-trematic rami in each of the three anterior branchial arches have not been observed in other Urodela. The anastomosis in the hyoid arch between the pre-trematic IX and a small nerve (my "facialis A") from the t. hyomandibularis is found also by DRÜNER in adult *Triton*. DRÜNER (p. 573) considers that this nerve may represent a vestigial, sensory r. post-trematicus of the facialis.

The anastomosis of the first branchial arch between the r. pre-trematicus of the first t. branchialis vagi and the twig from the t. glossopharyngeus, which is the strongest and most constant of the series in *Amblystoma*, may be comparable to an anastomosis between the pre- and post-trematic nerves of the first branchial arch in *Amia* (ALLIS, '97, p. 687) and in *Menidia*

(HERRICK, '99, p. 257). It is doubtful, however, that there is any genetic relationship between these anastomoses in Urodela and fishes.

It may be of interest, also, to notice the parallelism which exists between the anastomoses just mentioned for *Amblystoma* and the well known anastomoses between the nerves which supply the external gills. The first gill, which is born upon the first branchial arch, receives a nerve which is formed by fusion of branches from the t. glossopharyngeus and the first t. branchialis X. The second gill, which is supported upon the second branchial arch, receives a nerve which is formed by fusion of branches from the first and second tt. branchiales X. The third gill receives a nerve from the second t. branchialis X which sometimes, probably typically, fuses with a branch from the second spinal. The parallelism between these two series of anastomoses is so striking that one is tempted to attribute it to some genetic relationship between the two series. Such an interpretation, however, would involve the assumption that my fifth branch of the first t. branchialis X and third branch of the second t. branchialis X are pre-trematic nerves. But these nerves are largely motor while the typical pre-trematic nerve is sensory only. Furthermore, the external gill is considered ectodermal in origin and not a derivative of the internal gill of the fish. I believe, therefore, that the anastomoses of the nerves to the external gills are the result of adaptation, and that the presence of a nerve from the first t. branchialis vagi in the first external gill, a structure born upon the first branchial arch, does not warrant the conclusion that the nerve is pre-trematic in function. If this conclusion is correct, the parallelism between the two series of anastomoses in question is only accidental.

6.—*Ram. Post-trematici.*

The relation of the t. glossopharyngeus to the m. cerato-hyoideus externus in Urodela has already been discussed in connection with the r. jugularis VII. The m. cerato-hyoideus

internus is innervated in *Proteus* and *Menobranchus* (DRÜNER, p. 451) wholly by the t. glossopharyngeus. In *Salamandra* and *Triton* larvae, and also in *Siredon*, according to DRÜNER, this muscle receives fibers from the plexus subceratobranchiales, a plexus which is formed by the fusion of the terminal ramuli of the r. post-trematici. In *Amblystoma* larvae, however, I have found no such plexus, and the m. cerato-hyoideus is innervated by the t. glossopharyngeus alone. DRÜNER maintains, also, that the t. glossopharyngeus participates in the innervation of the first m. levator branchii. I have not found such a condition in any of my specimens.

In *Salamandra* larvae, DRÜNER (p. 500) has described a peculiar nerve which he calls "N. cutaneus retrocurrens IX." This nerve arises from the t. glossopharyngeus, or the r. post-trematicus IX, in the region of the m. cerato-hyoideus internus, penetrates this muscle ventrad and later the m. interhyoideus also. After passing through the latter muscle it inclines more laterad subcutaneously and is distributed "zu einer Reihe von knospenförmigen Sinnesorganen."

This observation of a branchial nerve innervating cutaneous sense organs in Amphibia is unique. It is unfortunate that DRÜNER has not given data by which the exact nature of these organs may be known. *A priori* they would be interpreted as belonging to the cutaneous terminal bud system, since no lateralis fibers are known to enter the t. glossopharyngeus in Amphibia. But the terminal buds are supposed to occur in the skin in fishes only. However, I have myself observed organs in the skin of *Amblystoma* in the region of the gills which have neither the typical appearance nor the typical innervation of lateral line organs. I have observed, also, that communis fibers probably go to the skin from the t. hyomandibularis, yet I have been unable to demonstrate conclusively the presence of terminal buds in the skin of *Amblystoma*. This observation of DRÜNER'S, however, makes it seem probable that such organs do exist in the skin of some larval Amphibia.

V. THE FIRST TWO SPINAL NERVES.

1.—*The Motor Component.*

In *Salamandra*, *Menopoma* and *Triton* DRÜNER finds spino-occipital nerves which arise within the cranium and unite with the ventral ramus of the first spinal nerve. These nerves are especially strong in *Triton*. Here they arise from the ventral side of the medulla caudally of the exit of the most caudal vagus root, in line with the ventral roots of the spinal nerves. A small branch passes dorsally of the ganglion IX+X to the dorsal muscles. The larger division passes through a distinct foramen beneath the occipital condyle and passes ventrally of the musculature to fuse with the ventral ramus of the first spinal nerve near the flexure of the latter cephalad.

DRÜNER does not find these nerves in *Menobranchus* and reports their occurrence in *Proteus* as doubtful. They do not occur in *Amblystoma*. On the other hand, instead of nerves from the region of the vagus to that of the first spinal, a branch from the first spinal passes cephalad across the dorsal surface of the ganglion IX+X to the musculature of that region.

With the exception of the occurrence of spino-occipital nerves in some species, the hypoglossal nerve in all Urodela seems to be formed as in *Amblystoma* by the fusion of the ventral, motor rami of the first two spinal nerves.

2.—*The Cutaneous Component.*

Ganglia are not found on the dorsal roots of the first two spinal nerves in all Urodela. DRÜNER finds a ganglion upon the root of the first spinal in larvae of *Salamandra*, and occasionally in the adult also. It is not so frequently found in larvae of *Triton*, and never in the adult. Neither is it found in *Proteus* and *Menobranchus*. In *Proteus* and *Menobranchus*, also, no ganglion is found on the root of the second spinal nerve. *Amblystoma* agrees closely with *Salamandra* and *Triton* in this respect, since the ganglion is well developed on the root of the first spinal nerve, and of variable occurrence on the root of the second.

In *Amblystoma*, sensory neurones of the second spinal nerve enter the ventral ramus and are distributed to the skin of the pectoral region. DRÜNER recognizes such neurones in the corresponding nerve of *Salamandra* and *Triton*, but gives no account of their distribution. It would have been instructive had he given, also, the distribution of the sensory neurones which no doubt pass into the ventral ramus of the third spinal nerve in *Proteus* and *Menobrachius* which have no ganglion on the second spinal nerve, for it is probable that these neurones have advanced into the territory which typically belonged to the second spinal nerve. If this supposition should prove correct it would be plain evidence in favor of the theory of "usurpation of nerves" (HERRICK, '99, p. 415) by which I have explained the peculiarities of the amphibian *r. alveolaris* VII and *r. mandibularis* VII. Indeed, it is obvious that in adult *Amblystoma* there is typically one segment, and in *Proteus* or *Menobrachius* two adjacent segments, without a spinal ganglion, and it is impossible to explain the cutaneous innervation of these segments without the presence of neurones from other segments. It seems necessary, therefore, to assume that one nerve, in the course of time, may usurp the function of the nerve of an adjacent body segment.

The branchial ramus of the second spinal nerve to the third external gill, which I have described for *Amblystoma*, has not been observed in other Amphibia.

VI. CONCLUSIONS.

1. The two elements of the olfactory nerve of *Amblystoma* represent the two roots of the nerve in *Gymnophiona* and *Triton*.

2. Because of the great variation which occurs in the peripheral relation of the eye-muscle nerves, great caution must be observed in dealing with the morphological significance of these relations.

3. The difference in the origin of the communis VII root in Urodela and Anura cannot be explained on the basis of correlated changes in the lateralis VII and auditory nerves. The relations of the geniculate ganglion in Siren is of obscure significance, but it may have important bearing on the morphology of the r. alveolaris and r. mandibularis internus.

4. The r. palatinus of Amblystoma, and probably of other Urodela, corresponds with the r. palatinus of the tadpole in the division posteriorly of the internal nares into two divisions each of which anastomoses with a general cutaneous branch of the trigeminus.

5. The r. ophthalmicus profundus of Amblystoma performs the function of the r. maxillaris and r. ophthalmicus profundus in the tadpole of the frog. The terminal rami of the r. ophthalmicus profundus in Amblystoma are not exact equivalents to those of the tadpole and should not have the same nomenclature as the latter.

6. The r. maxillaris of Urodela is homologous with the "accessory" branch of the trigeminus in the tadpole, and both these nerves probably represent the r. maxillaris of fishes much diminished in function.

7. The lateral line nerves, r. ophthalmicus superficialis, r. buccalis and r. mentalis, appear to be remarkably constant in Urodela. They are derived from the lateralis VII root.

8. The r. alveolaris is a pre-spiracular nerve and is not the homologue of the r. mandibularis internus of Anura and fishes. The latter nerve is post-spiracular.

9. The sensory part of the r. post-trematicus VII may be represented occasionally in some Urodela by a small nerve which anastomoses with the r. pre-trematicus IX.

10. WILDER's *posterior palatine* of Siren is of doubtful significance. It may not represent the r. palatinus caudalis of Amblystoma.

11. The most cephalic root of the IX+X complex in Urodela is the lateralis X root. It fuses quickly with the root of the glossopharyngeus. The posterior root of the complex is the n. accessorius of higher vertebrates.

12. There is no constant arrangement in *Amblystoma* of the roots of the vagus into a particular number of rootlets which can be compared with the arrangements described by some authors in other Urodela. In composition the roots of the vagus are constant throughout the Amphibia, in so far as they have been adequately studied.

13. The r. supratemporalis of *Amblystoma* corresponds to the nerve of the same name in the tadpole of the frog. The nerve has been misinterpreted by BOWERS in *Spelerpes* and by DRÜNER in *Menobranchus*.

14. The rr. laterales superior and inferior are constant in their relations in all the Urodela. The r. lateralis inferior has been wrongly figured as a motor nerve by BOWERS.

15. The r. communicans IX+X ad VII, in so far as it is general cutaneous, corresponds to the nerve of the same name in *Anura*. It differs from the latter nerve, however, in having a communis component. The composition of the nerve in *Amblystoma* speaks strongly against DRÜNER's interpretation of the r. communicans in other Urodela.

16. JACOBSON's anastomosis does not appear in *Anura* and is wanting also in some Urodela. The relation of this anastomosis to the JACOBSON's anastomosis of fishes is doubtful.

17. The nerves to the external gills should not be classed with the pre-trematic and post-trematic nerves.

18. The pre trematic nerves of *Amblystoma* are typical for Urodela, and indicate a closer affinity between the innervation of the gill clefts in Amphibia and that in fishes than has been otherwise demonstrated.

19. There is no plexus subceratobranchiales in *Amblystoma* like that described by DRÜNER for other Urodela. The N. cutaneus retrocurrens IX of DRÜNER in *Salamandra* increases the probability which appears in *Amblystoma* that there are terminal buds in the skin of some larval Urodela.

20. The hypoglossal nerve is formed in all Urodela by the fusion of the ventral motor branches of the first and second spinal nerves, and in some species by the addition of spino-occipital nerves. The roots of all these nerves arise

from the ventral side of the medulla or cord as typical ventral spinal roots.

21. Ganglia may or may not occur on the roots of the first and second spinal nerves in Urodela.

22. I have found no evidence that the lateral line organs of *Amblystoma* are innervated by any but lateralis fibers from the lateralis roots of the seventh and tenth nerves. The fibers of this system are large and heavily medullated.

23. The variations, which are described in Part First, in the relations of the eye-muscle nerves, in the r. palatinus, in the roots of the nerves, and in other cases not described in the text, show that great caution should be exercised in researches upon the nervous system of Urodela not to record accidental variations as constant characteristics of the species. Especially is this true in the study of young larvae, in which many of the organs are in an extremely transitory state.

24. The components of the cranial nerves of *Gymnophiona*, *Amphiuma*, *Siren*, and other Urodela are not adequately known. Dissections show that in these forms there are important features which must be accurately worked out before the morphology of important rami of the amphibian facialis and trigeminus can be properly understood.

Brown University, March 31, 1902.

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DESCRIPTION OF FIGURES.

REFERENCE LETTERS.

- alv. VII.*—ramus alveolaris VII.
- alv. a.*—branch of latter found in one specimen.
- aur.*—ramus auricularis vagi.
- aur. 1.*—anterior branch of latter.
- aur. 2.*—posterior branch of same.
- aur. 1a.*—branch of *aur. 1.* to near first gill.
- b. VII.*—ramus buccalis VII.
- ch. ex.*—nerves to the m. ceratohyoideus externus.
- ch. ex. + mhp.*—nerves to the mm. ceratohyoideus externus and inter-hyoideus.
- com. IX + X ad VII.*—ramus communicans IX + X ad VII.
- dm.*—nerves to the m. depressor mandibulae.
- fA.*—facialis A.
- gc.*—general cutaneous branches of the r. jugularis VII.
- g. sp. 1.*—ganglion of the first spinal nerve.
- hgl.*—N. hypoglossus.
- hmd.*—truncus hyomandibularis VII.
- int.*—ramus intestinalis vagi.
- IX.*—root of the glossopharyngeus.
- IXt.*—truncus glossopharyngeus.
- IX, 5, 6, 7, 8, 9.*—fifth, sixth, seventh, eighth and ninth branches respectively of the t. glossopharyngeus.
- jgl. VII.*—ramus jugularis VII.
- li.*—ramus inferior.
- lop.*—lateral terminal branch of the r. ophthalmicus profundus V.
- lp.*—lateral terminal branch of the r. palatinus VII.
- l. s.*—ramus lateralis superior.
- lsd.*—dorsal branch of latter.
- mdb.*—ramus mandibularis trigemini.

mdb. 1, 2, 3, 4.—first, second, third and fourth branches respectively of *mdb.*

mdb. 2a.—branch of same to inner epithelium of cheek.

mdb. 2b.—branch of *mdb. 2.* to skin.

mdb. 4a.—branch of fourth mandibular ramus to the r. alveolaris VII.

mdb. 4b.—branch of fourth mandibular ramus to the skin of mandible.

mhp.—nerves to the m. interhyoideus.

mhp. V + VII.—nerves of the trigeminus and facialis to the m. interhyoideus.

mop.—mesial terminal branch of the r. ophthalmicus profundus trigemini.

mp.—mesial terminal branch of the r. palatinus VII.

mtl.—ramus mentalis VII.

mtl. ex.—r. mentalis externus.

mtl. in.—r. mentalis internus.

mxv.—ramus maxillaris trigemini.

op. V.—ramus ophthalmicus profundus trigemini.

op. V. 2, 3.—second and third branches of the latter.

o. s. VII.—ramus ophthalmicus superficialis facialis.

p. VII.—ramus palatinus facialis.

p. c. VII.—ramus palatinus caudalis facialis.

p. c. VII + IX.—nerve from JACOBSON'S anastomosis.

prt. IX.—ramus pre-trematicus glossopharyngii.

prt. X. 1.—ramus pre-trematicus of first t. branchialis vagi.

prt. X. 2.—ramus pre-trematicus of second t. branchialis vagi.

prt. X. 3.—ramus pre-trematicus of third t. branchialis vagi.

pst. IX.—ramus post-trematicus glossopharyngii.

pst. X. 1.—ramus post-trematicus of first t. branchialis vagi.

pst. X. 2.—ramus post-trematicus of second t. branchialis vagi.

rec.—ramus recurrens vagi.

rec. 1, 2, 3.—first, second and third branches respectively of ramus recurrens vagi.

spt.—ramus supratemporalis vagi.

sp. 1.—root of first spinal nerve.

sp. a, b.—two rootlets of latter.

sp. 1. d.—dorsal branch of first spinal nerve.

sp. 1. r. 1.—first branch of first spinal nerve.

sp. 1. v.—ventral branch of first spinal nerve.

sp. 2. v.—ventral branch of second spinal nerve.

sp. 2. va.—cutaneous branch of ventral ramus of second spinal nerve.

V.—root of trigeminus.

VII. l.—lateralis root of facial nerve.

• *VII. c.*—communis root of facial nerve.

VII. m.—motor root of facial nerve.

v. o. p. V.—ventral terminal branch of r. ophthalmicus profundus V.

vsc.—truncus visceralis vagi.

vsc. 1.—first branch of t. visceralis vagi.

vsc. 1a.—branch of latter to mm. cucullaris and dorso-trachealis.

X. 1.—lateralis root of vagus.

X. 2, 3, 4.—second, third and fourth roots respectively of the vagus.

X. 4. a, b, c, d.—rootlets of the fourth root of vagus which are variable.

X. 1br.—first truncus branchialis vagi.

X. 2br.—second truncus branchialis vagi.

X. 1br. 1, 5, 6, 7, 8, 9, 10.—first, fifth, sixth, seventh, eighth, ninth and tenth branches of first t. branchialis vagi.

X. 2br. 3, 4, 5, 7, 8.—third, fourth, fifth, seventh and eighth branches respectively of the second t. branchialis vagi.

PLATE XV.

Fig. 1. A projection of the roots and ganglia of the fifth, seventh, ninth, tenth and first two spinal nerve of *Amblystoma* upon the horizontal plane. This projection is made to scale from serial sections of the head.

PLATE XVI.

Fig. 2. A projection of the cranial nerves of *Amblystoma* on the sagittal plane. This projection is made to scale from serial sections of the head. In the figure as it is here presented it has been necessary to modify the position of some nerves in order not to obscure others. The trunk of the glossopharyngeus as it passes backward and downward is pushed downward from its actual position in order to bring the t. visceralis into view. The order of branching of the fifth, sixth and seventh branches of the first branchial X trunk has been changed for sake of clearness in their peripheral relations. The actual course of *1st*, also, is modified in relation to other nerves. These, and other slight alterations in the relative position of nerves, do not change the essential relations of the components which it is the prime purpose of the projection to show.

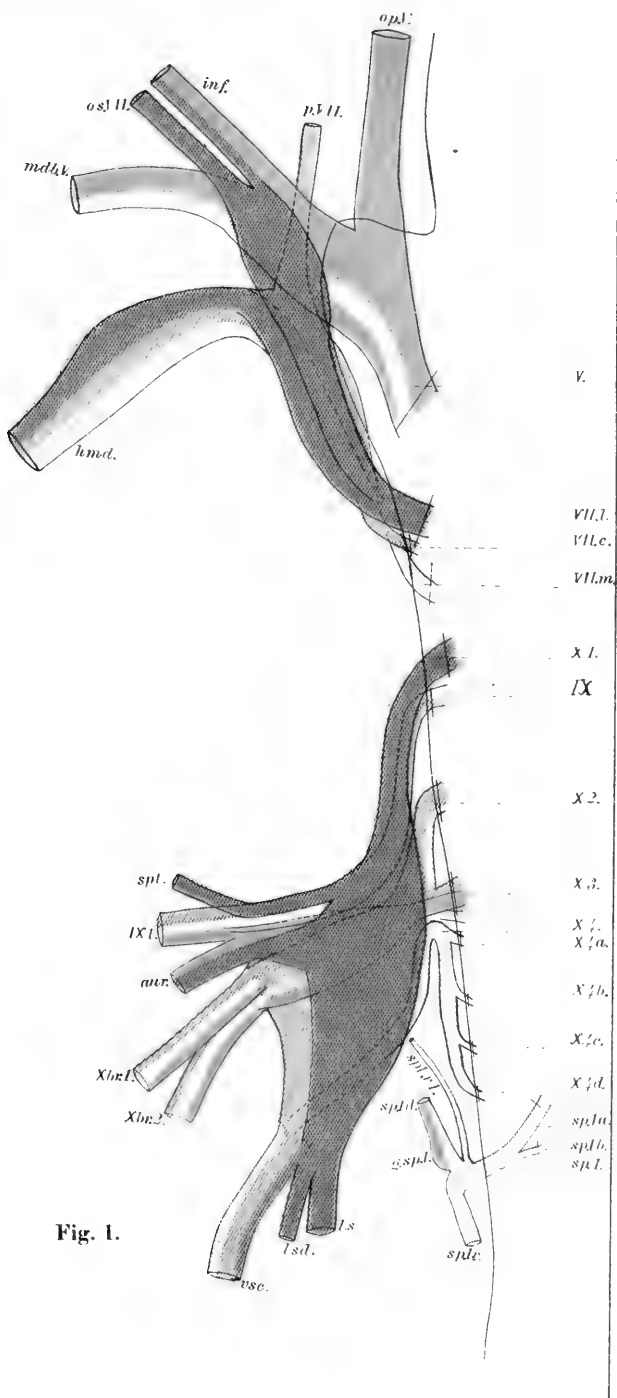
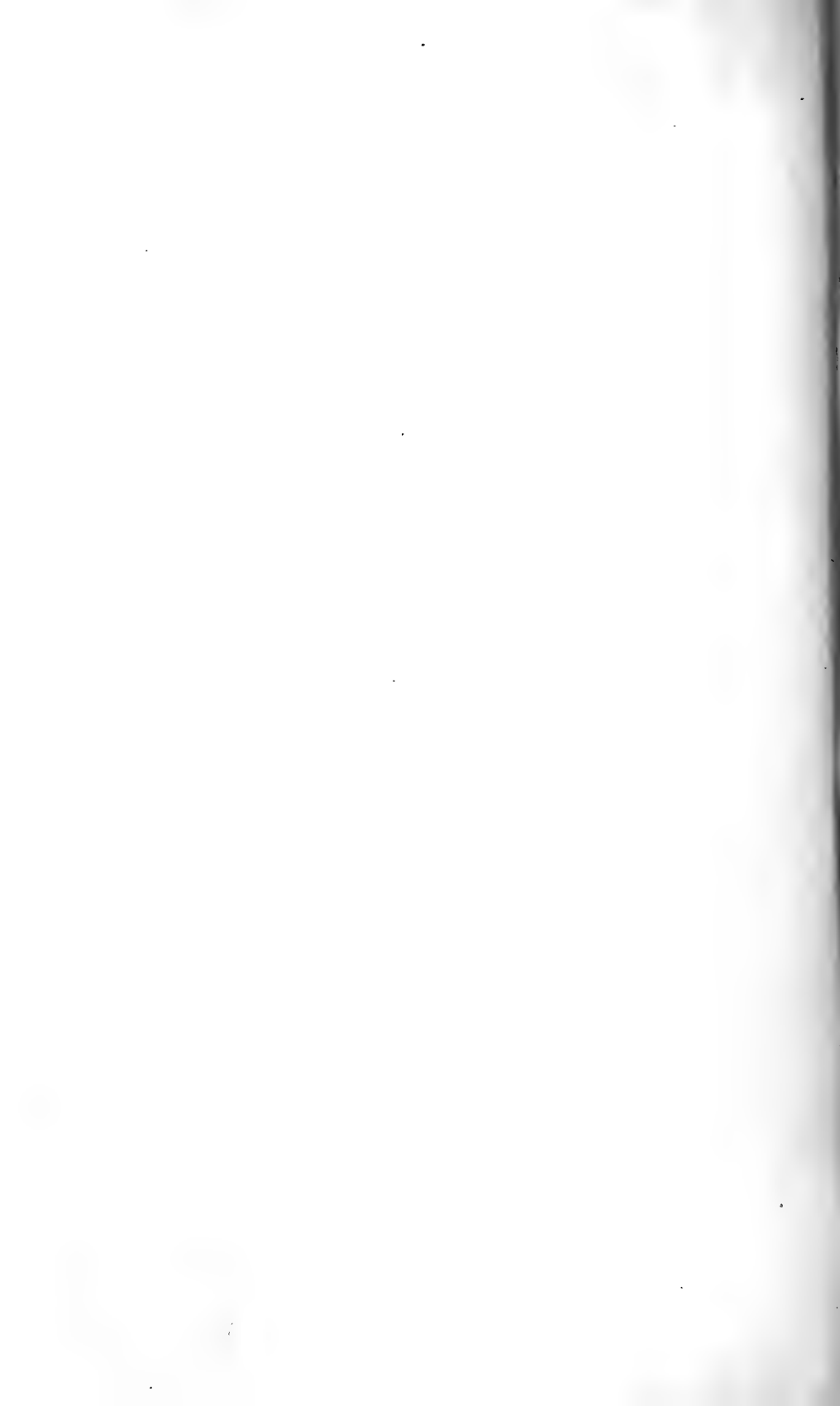


Fig. 1.





Fig. 2.



THE
JOURNAL OF COMPARATIVE NEUROLOGY.

ON THE ORIGIN OF NEUROGLIA TISSUE FROM
THE MESOBLAST.

By SHINKISHI HATAI.

(From the Neurological Laboratory of the University of Chicago.)

With Plate XVII.

It is now generally believed that the neuroglia cells in the central nervous system are produced by cell division from either germinal cells in the ectoderm which lines the primitive neural canal or from their direct descendants. In other words, all the neuroglia cells, as well as the nerve cells, have the same origin, both arising from the ectoderm.

Opposed to this idea is the report of CAPOBIANCO and FRAGNITO ('98) of a second source of the neuroglia, namely the mesoblast. According to them, in an early embryonic stage, a large number of the mesoblastic cells forming the meninges migrate into the central nervous system or are carried in by the blood capillaries, and finally become transformed into the neuroglia cells. This conclusion was reaffirmed very recently by CAPOBIANCO ('01) and his observations further extended.

While the present writer was examining the preparations of embryonic brains of various animals, his attention was drawn to the fact that the neuroglia cells are produced not only in the manner reported by CAPOBIANCO and FRAGNITO, but that a large number of these cells, in a later embryonic stage, are formed by the proliferating cells of the capillary walls. The conclusion that some of the neuroglia cells are derived from the capillary walls is based on the following observations.

The materials used for the investigation were white rats having body-weights of 3.5 and 4.5 grams respectively, and

mice killed just after birth (body-weight unknown). The material was preserved with CARNOY's mixture, and imbedded in paraffin according to the usual procedure. The sections were cut 6μ thick, and stained with a saturated aqueous solution of thionin followed by 1% eosin in 70% alcohol. Besides these, sections of the cord from man and the dog, treated with WEIGERT's neuroglia stain, were used for comparison.

For this investigation, the section of a region of the pons was examined for the reason that owing to the small number of nerve cells, the capillaries were there less abundant and easier to observe. In this locality it is possible to follow various stages of the migration of the proliferated cells of the capillary wall into the brain substance. Around the capillaries a collection of nerve cells and neuroglia nuclei are clearly visible (Figs. 1, 2, 3, 5, 6). The nerve cells are well developed and the protoplasmic processes, as well as the stainable substance in the cytoplasm, may easily be demonstrated. In the case of the neuroglia, however, the nuclei only are well defined, the cytoplasm being less differentiated and probably small in amount. Although the nuclei of the neuroglia cells exhibit considerable variation, a careful observation reveals that they are represented by two distinctly characterized types. The following description aims to present the main characters of the two types just mentioned.

1. Size. As determined by the longest diameter, the nucleus of the type "b" which measures 9.5μ , both in white rat and mouse, is much longer than that of the type "a" which measures 8.3μ , in the white rat and 7.4μ in the mouse. Each of the above diameters was obtained by taking an average from the measurement of ten nuclei.

2. Form. The external form of the nuclei is one of the important features for a classification into two types. One form (type a) of the nuclei presents a more or less circular or a slightly oblong shape (Fig. 9), while the other (type b) shows a more oblong or spindle form. A characteristic appearance of this type "b" is that of a wavy outline of the nucleus or in some cases an amoeboid form.

3. Staining characters. The manner of staining is more important for a distinction of the two types. Type "a" stains very faintly with the eosin, while the type "b" shows stronger affinity for this reagent. The difference in staining between the two forms is quite evident in both the white rat and mouse.

Some of the previous investigators (WEIGERT, MALLORY, HUBER) who examined the neuroglia tissue, noticed two varieties of nuclei, one staining more deeply than the other. It is however not easy to identify either of their forms with those here described.

4. Internal structure of the nuclei. This is the most important feature for the classification of the nuclei into two types. In type "a," the nucleolus is always distinctly visible lying in or near the center of the nucleus. It takes a basic stain like the nucleolus of the nerve cells. The acidophile particles which hang on the filaments of the linin reticulum are less numerous than in the case of type "b." The arrangement or distribution of the acidophile particles, as well as the distinct formation of a linin network, is exactly similar to that of the nerve cells (Fig. 9). The latter (type b) however, presents just the opposite characters to type "a." As a rule the nucleolus and linin network are not visible. Exceptional cases where the nucleoli and linin substance were present in type "b," have been observed several times. In these cases, however, the reticular formation is peculiar to this type, and entirely different from that in type "a." Further, the large number of the acidophile particles aggregated along the periphery of the nuclei indicates plainly that these peculiar nuclei are merely a modification of the type "b." The size of the acidophile particles in type "b" is variable, some of them being very large. These large particles—the nucleoli—are probably due to the fusion of several smaller particles.

From the above description it is concluded that in the developing nervous system of these animals, the neuroglia nuclei may be divided into two types according to their form, staining characters and internal structure.

The question arises at once concerning the origin of the

two types of the neuroglia elements just mentioned. From the previous descriptions, the origin of the type "a" from the ectoblast will be easily explained, since it exhibits a close similarity to the nuclei of the nerve cells. An explanation of the origin of the cells of the type "b," however, is difficult, for they have none of the structural characters of the ectoblast cells. For the solution of this problem, attention was directed to the structure of the nuclei of the capillary wall.

The capillary wall is composed of a single layer of the endothelial cells (Figs. 1, 2, 3, 4, 5, 6, 7). An outline of an individual cell, however, can not be made out by the technique employed for the present investigation. The nuclei, however, as can be seen in most cases, are placed very close together, while in some cases, a long space appears between the two nuclei (Fig. 6). In other cases, the nuclei are placed so closely that the one partly overlaps the other (Fig. 4). The external form of these nuclei shows considerable variation, as will be seen from the figure 8, as well as from the other figures (Figs. 1, 2, 3, 4, 5, 6, 7). This is due in part to the plane in which the nucleus has been sectioned. Curiously enough, the shape and size of the nuclei of the capillary wall coincide very closely with that of the nuclei of the neuroglia nuclei which belong to the type "b;" that is, it appears oblong, somewhat spindle shaped as well as flattened from side to side. The only form of the type "b" not found in the capillary wall is that which appears like an amoeba in motion. An examination of the internal structure of the nuclei in the capillary wall reveals still other points of similarity as shown by the numerical relations, as well as the peripheral aggregation of the acidophile particles, the absence of the nucleoli and linin filaments, and a strong affinity for the acid dyes. In these particulars it coincides exactly with the nuclei of the type "b" of the neuroglia. The writer was unable to see any structural differences between these two forms just mentioned; this suggests a close connection between them.

On examining the capillary wall, the writer noticed, very frequently, a nucleus projecting outwardly (Figs. 1, 2, 5, 6), and in some cases, these nuclei were isolated from the capillary

wall, but lay close to it (Fig. 7). Between these two appearances, various intermediate stages could be easily found. In some cases a tip of the nucleus is still attached to the capillary wall, while the rest of it has become separated (Figs. 5, 6). This appearance suggests very strongly the migration of the nucleus from the capillary wall into the surrounding tissue. It is known that leucocytes escape from the capillary wall and exhibit amoeboid movements, but their nuclei are easily distinguished from those of the endothelial cells by their structure as well as their size; the former being very much smaller than the latter.

As soon as the nuclei are separated from the capillary wall, they become amoeboid and migrate away from the capillary. The following observation is in favor of the above conclusion. A large number of the mitotic figures of various phases in the nuclei of the capillary wall are often visible. In such a locality where the mitoses are abundant, the nuclei are so closely placed that in some cases, the one nucleus overlaps the other the outermost nucleus projecting outwardly, thus showing the first step of the migration.

From these observations the conclusion is drawn that the neuroglia nuclei in the white rat as well as in the mouse represent two distinctly characterized types; namely, nuclei the structure of which resembles very closely that of the nerve cells (type a), and the nuclei, the structure of which resembles very closely that of the endothelial cells which form the capillary wall (type b). These two types of nuclei have been derived from the ectoblast and the mesoblast respectively. The latter (type b), has probably two sources of origin; that is, they are partly derived from mesoblastic cells immigrating from the meninges (CAPOBIANCO and FRAGNITO), and partly from proliferating endothelial cells of the walls of the capillaries, these cells having separated from the capillary wall and migrated into the surrounding tissue, where they constitute one type of the neuroglia elements.

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ILLUSTRATIONS.

The following are free-hand drawings made by the aid of o.c. 4, obj. 1-12 of Bausch & Lomb Company. In all cases *a* indicates the nuclei of the type "a;" *b* indicates the nuclei of the type "b;" *c* indicates nerve cells and *d* indicates a capillary.

Fig. 1 Showing distribution of the nerve cells (*c*), neuroglia nuclei (*a*, *b*) and blood capillaries (*d*) mouse.

Fig. 2. Showing nuclei (*b*) partly separated from the capillary wall (*d*) mouse.

Fig. 3. Showing distribution of the two types of neuroglia nuclei (*a*, *b*) mouse.

Fig. 4. Showing mitotic figures in "b" mouse.

Fig. 5. Showing several stages of separation of the nuclei (*b*) of type "b" from the capillary wall white rat.

Fig. 6. Showing one projecting and one partly isolated nucleus (*b*) white rat.

Fig. 7. Showing the advanced stage of projection of the nucleus (*b*) from the capillary wall (*d*) white rat.

¹*Fig. 8.* Showing five typical endothelial nuclei (*b*) mouse.

¹*Fig. 9.* Showing three typical ectoblastic nuclei (*a*) mouse.

¹ Figs. 8 and 9 were drawn with the same enlargement.

ON THE NUMBER AND ON THE RELATION BETWEEN DIAMETER AND DISTRIBUTION OF THE NERVE FIBERS INNERVATING THE LEG OF THE FROG, *RANA VIRESCENS* BRACHYCEPHALA, COPE.

BY ELIZABETH HOPKINS DUNN, M. D.

(From the Neurological Laboratory of the University of Chicago.)

With two figures in the text.

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SUMMARY.

1. A comparison of the gross nerve supply to the leg shows no marked differences between *Rana esculenta* and *Rana virescens*.

2. In the branches both to the thigh and the shank of *Rana virescens* the number of fibers observed exceeds the number calculated. This excess seems to be due to dividing fibers. In teased preparations such dividing fibers have been observed occurring near the points where branches are to be given off.

3. A constant increase in the number of fibers at successive levels of the sciatic where no branches are given off indicates that fibers divide within the nerve trunk.

4. The proportional number of muscular and cutaneous fibers varies quite widely in different frogs, while for the two legs of the same frog the proportions are similar.

5. The diameter of the largest fibers going to the different segments of the leg diminishes in regular order from thigh to foot. Hence, for the leg of *Rana virescens* at least, it is true that the largest fibers run the shortest course. The conclusion of SCHWALBE that the largest fibers run the longest course has been shown to be unsupported by his observations.

6. A confirmation of the theory of the conical diminu-

tion of the nerve fiber in its course is found in the constantly decreasing average area for the nerve fibers at successive levels in a region where no branches arise.

7. In this series of observations it has always been found that in a cross section of a nerve the area of the axis cylinder was approximately equal to the area of the medullary sheath—therefore all the observations made upon the area of the fiber as a whole can be expressed in terms of the more functionally active portion—the axis cylinder.

INTRODUCTION.

The innervation of the thigh in the frog, *Rana virescens* brachycephala, Cope, has been quite fully discussed in a paper, DUNN, 1900, which embodied the results of a study carried on in this laboratory. The present study is an attempt to verify the results then obtained by a repetition of the investigation for the thigh branches and a further determination of the number and diameter of the fibers innervating the shank and the foot.

This present investigation contains data based upon a study of the right and left hind extremities of a single frog. The results obtained from the two sides, while acting as mutual controls, are of further value in illustrating the similarity of innervation for the right and left sides of the same individual.

SECTION I. Gross Anatomy of the Muscular and Cutaneous Nerves Supplying the Thigh and the Shank.

The VIIth, VIIIth and IXth¹ spinal nerves unite to form the plexus lumbo-sacralis from which the skin and muscles of the hind extremity of *Rana virescens* receive their innervation. From this plexus the fibers pass to their destination by way of two main nerve trunks, the crural and the sciatic nerves. The crural nerve, the smaller of these trunks, sends branches only to the thigh. The sciatic nerve, the larger of the trunks, con-

¹ GAUPP designates these nerves as the VIIIth, IXth and Xth, numbering the spinal nerves from II to XI, inclusive. See GAUPP's edition, ECKER's and WIEDERSHEIM's *Anatomie des Frosches*, Part II, p. 156.

veys the chief mass of fibers to innervate the hind extremity, and innervates the thigh, shank and foot. After giving off its branches to the thigh it divides in the lowest third of the thigh into the tibial and the peroneal nerves. The tibial nerve divides just below the knee to form what are known as the rami superficialis et profundus of the tibial nerve. The peroneal nerve divides near the middle of the shank into the nervus peroneus lateralis and the nervus peroneus medialis.

The skin and muscles of the thigh, therefore, are innervated by branches from the crural and the sciatic nerves; the muscles and skin of the shank by branches from the tibial and peroneal nerves and their divisions; and the tissues of the foot by the terminal branches from the first and second subdivisions of the tibial and peroneal nerves.

A. Comparison of Rana virescens with Rana esculenta and Rana temporaria.

In the previous study, DUNN, 1900, of the innervation of the thigh, adoption was made of the nomenclature used by GAUPP in his late edition of ECKER and WIEDERSHEIM's Anatomy of the Frog, to identify the muscles and the nerve branches. The same authority will be followed in the anatomical nomenclature used in this paper.

A comparison of the gross innervation of the thigh in *Rana virescens* with that of *Rana esculenta* and *Rana temporaria* revealed a few minor variations. A similar comparison of the gross innervation for the shank reveals a correspondingly small number of differences.

Tables I and II are presentations in brief of the nerve branches to the thigh and to the shank.

Table I contains only the main branches of the crural and sciatic nerves to the thigh, and the designations by which they may be identified in Figure 1. A more complete tabulation with an accompanying figure may be found on pp. 220 and 221 of the preceding study, DUNN, 1900.

TABLE I.

Tabulation of the chief Nerve Branches passing to the Skin and Muscles of the Thigh in *Rana virescens brachycephala*, Cope.

- C. Nervus cruralis s. N. femoralis anterior.
 - a) Ramus cutaneus femoris lateralis.
- S. Nervus ischiadicus s. N. femoralis posterior.
 - 2. R. cutaneus femoris posterior.
 - 3. R. muscularis to the M. pyriformis.
 - 4 and 5. Rr. musculares to the M. gemellus and the M. obturator internus.
 - 6. R. profundus posterior.
 - 7. R. muscularis to the M. ileo-femoralis.
 - 8. R. profundus anterior.
 - [x. R. muscularis to the M. ileo-fibularis.]

Table II is a presentation of all the nerve branches to the shank. GAUPP's designations are used for these tables and for Figure 1.

Figure 1 is a dorsal view of the right plexus lumbosacralis of *Rana virescens*, and includes all the ramifications from the point where the spinal nerves emerge from the vertebral foramina, to a point opposite the ankle. The attempt has been made to represent in this figure the relative sizes of the trunks and branches, and the points and order of branching.

TABLE II.

Tabulation of the Nerve Branches passing to the Skin and Muscles of the Shank in *Rana virescens brachycephala*, Cope.

- T. Nervus tibialis.
 - α. Ramus cutaneus cruris posterior.
 - β. R. muscularis for the M. plantaris longus.
 - 1. R. superficialis of the N. tibialis.
 - a. R. muscularis to the M. plantaris longus.
 - b. R. cutaneus cruris medialis inferior.
 - 2. R. profundus of the N. tibialis.
 - a. R. cutaneus cruris medialis superior.
 - b. Rr. musculares for the M. tibialis posticus.
- P. Nervus peroneus.
 - a. R. articularis genu et pedis.
 - α. R. articularis genu.
 - β. R. articularis pedis.
 - b. R. cutaneus cruris lateralis.
 - c. R. muscularis to the M. extensor cruris brevis.
 - d. Rr. musculares to the M. peroneus.
 - 1. N. peroneus lateralis.
 - a. Rr. musculares to the M. tibialis anticus longus.
 - 2. N. peroneus medialis.
 - a. R. muscularis to the M. tibialis anticus longus.
 - b. Rr. musculares to the M. tibialis anticus brevis.

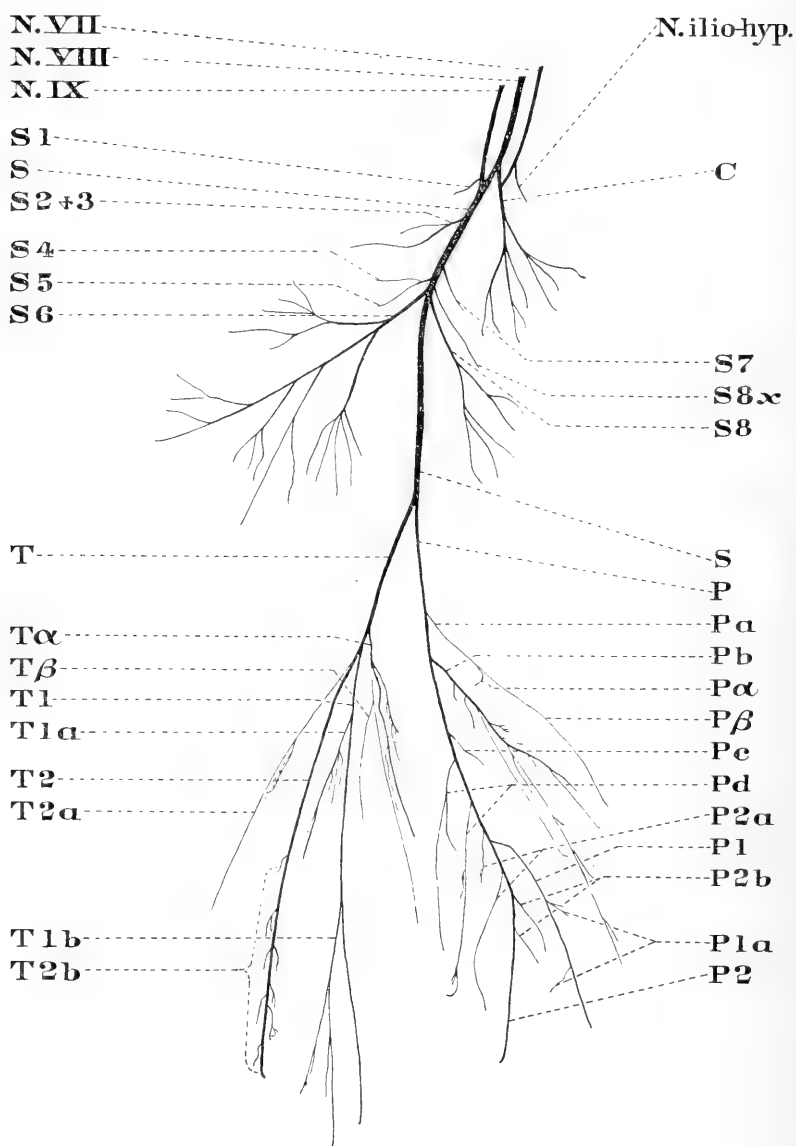


FIGURE I.

The musculature of the shank is so much more simple than that of the thigh that a comparison of the different accounts of the innervation of the shank as found in successive editions of ECKER is not deemed necessary. But as GAUPP has introduced new names for two of the six muscles of the shank, a brief tabulation of the muscles as named by ECKER and GAUPP is here appended.

TABLE III.

GAUPP's Edition of ECKER. 1896—1901	ECKER's Anatomie des Froches, 1864 HASLAM's translation, 1889.
Muscles of the calf.	
M. plantaris longus.	M. gastrocnemius.
M. tibialis posticus.	M. tibialis posticus.
Muscles of the extensor aspect.	
M. peroneus.	M. peroneus.
M. tibialis anticus longus.	M. tibialis anticus.
M. extensor cruris brevis.	M. extensor cruris brevis.
M. tibialis anticus brevis.	M. flexor tarsi anterior.

i. Variations appearing in successive dissections of *Rana virescens*.

In both the thigh and the shank the order in which the branches leave the main trunk presents little variation in different individuals, but the number and size of the branches vary more frequently in the shank than in the thigh. This condition is probably due to the fact that, while in the thigh a small number of large branches is given off within a short distance and these large branches subdivide to innervate many muscles, the branches to the shank separate at many points along the course of the nerve trunks and supply single muscles or send numerous branches to one muscle.

The large number of branches sometimes given off to single muscles is indicated in Table IV, which is a tabulation of the muscular and cutaneous nerve branches to the shank, as found in the frog designated as Frog II B, whose peripheral nervous system furnished material for the data discussed at a further point in this study.

TABLE IV.

Tabulation of the muscular, cutaneous and articular nerve branches to the shank in Frog II B.

Muscular branches.

	No. of branches.
From the Tibial nerve.	
Plantaris longus.	2.
Tibialis posticus.	8.
From the Peroneal nerve.	
Extensor cruris brevis.	2.
Peroneus.	2.
Tibialis anticus longus.	6.
Tibialis anticus brevis.	2.

Cutaneous branches.

From the Tibial nerve.
R. cutaneus cruris posterior.
From R. superficialis of the Tibial nerve.
R. cutaneus cruris medialis inferior.
From R. profundus of the Tibial nerve.
R. cutaneus cruris medialis superior.
From the Peroneal nerve.
R. cutaneus cruris lateralis.

Articular branches.

From the Peroneal nerve.
R. articularis genu et pedis.

2. Differences between *Rana virescens* and the standard furnished by *Rana esculenta*.

As has already been stated, the method of ramification of the shank branches varies greatly in the different frogs. This being the case, it has been difficult, even after a large number of dissections, to fix a standard for comparison with the standard adopted by GAUPP for *Rana esculenta*. The conditions most frequently present in the ten dissections already made have been indicated in Figure 1. Further dissections may reveal that some of the differences which seem to be constant are only accidentally coincident in these dissections. While this possibility of error is annoying in an attempt to make a statement as to fact, yet in the pursuance of an investigation such as the one here undertaken a variation of this character has no importance. Before any study was made of the number of fibers of any nerve branch, that branch was identified as supplying a certain muscle

or a certain cutaneous region, irrespective of its method or point of separation.

The differences in the innervation of the shank between *Rana virescens* and *Rana esculenta* are in detail as follows.

The branch designated in Figures 1 and 2 and Table II as T_β which in *Rana esculenta* is given off directly from the tibial nerve, in *Rana virescens* is given off with T_α , the ramus cutaneus cruris posterior. This branch T_β is one of the branches innervating the M. plantaris longus. A similar joining of a muscular and a cutaneous branch is found in the thigh in the instance of S_2 and S_3 which in *Rana virescens* are frequently given off together.

2. One branch to the M. tibialis anticus longus is given off from the main trunk of the N. peroneus in addition to those branches arising from the N. peroneus lateralis and the N. peroneus medialis. In *Rana esculenta* all the fibers supplying the M. tibialis anticus longus pass by way of the N. peroneus lateralis or the N. peroneus medialis.

SECTION II. Number and Diameter of the Nerve Fibers Innervating the Thigh, Shank and Foot.

A. Introduction.

The results obtained from a series of observations undertaken to ascertain the number and diameter of the fibers innervating the thigh made probable the deduction that, contrary to the long accepted statement of SCHWALBE, 1882, the largest nerve fibers do not run the longest course and so innervate the foot, but pass at a comparatively high level to innervate the tissues of the thigh.

This deduction rests upon two ascertained facts. The first is that the average area for the nerve fibers at the level just above the thigh branches, S_1 Figure 2, is greater than that for the fibers at a level just below the thigh branches, S_2 Figure 2, and is less than the average area for the fibers of the thigh branches. The second fact is that by actual measurements of the ten largest fibers in each of these three regions it was ascertained that the very large fibers that are present above the

thigh branches cannot be found in the sciatic nerve at a level below the thigh branches, but do appear among the fibers passing by the branches to the thigh.

These two facts pointed so strongly to the necessity for a revision of our beliefs regarding the destination of the largest nerve fibers and the interpretation of the variations in the size of nerve fibers that a more complete study of the number and diameter of the nerve fibers at stated levels, increasing in distance from the spinal cord, seemed very desirable. A study of the fibers in the branches to the thigh and to the shank was also fortunately completed upon the same frog, thus giving data for comparison which were all obtained from a single specimen.

So many very small branches required to be sectioned in this examination that a frog of the maximum size was selected.

The choice in this second series of observations fell upon a frog, designated as Frog II B, female, corrected weight 61.5 grams, length 234 mm. Both the enumeration of the fibers and the calculation of the areas were carried through for the right and left hind extremities.

1. Levels at which observations were made.

The exact points at which observations were made are indicated in Figure 2 by the breaks in the continuity of the nerve trunks and branches. Figure 2 is a reproduction of the main branches shown in Figure 1. The designations are those used for Tables I and II and Figure 1, with the addition of S_1 , S_2 , and $T + P$, to indicate the levels on the main trunks at which sections were made.

The levels on the main trunks chosen for comparison were four; the first at the point just above the branches to the thigh, indicated by C and S_1 ; the second at a point just below the thigh branches at S_2 . The data furnished by the section at S_2 , just above the point of division of the sciatic nerve, acted as a control upon the results obtained at S_1 . The third level was at a point just above the branches to the shank, cutting the tibial and peroneal nerves at T and P. The section at $T + P$, the immediate point of division of the sciatic nerve, fur-

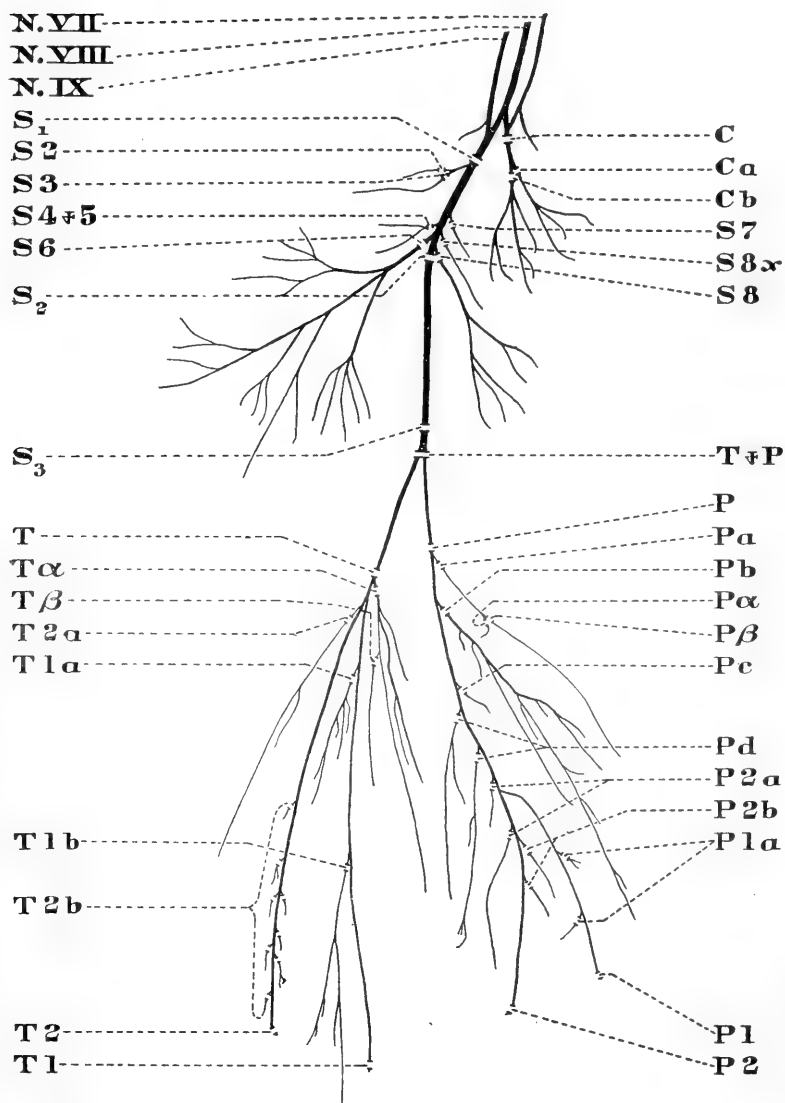


FIGURE 2.

nished control results for this third set of observations. The fourth level was at the ankle. At this point four trunks, T₁, T₂, P₁, and P₂, the subdivisions of the tibial and peroneal nerves, were sectioned.

The branches to the thigh and to the shank were sectioned as close as possible to their points of separation from the main trunks, as is indicated in Figure 2.

2. Methods of observation.

The methods of observation followed in this work varied but slightly from those used in the preceding study, DUNN, 1900. As soon as possible after the frog was chloroformed and its weight and length ascertained, the nerve tissue at the chosen levels was laid bare, the overlying tissues being so carefully separated that the nerve tissue was undisturbed. Into the cup-like cavity of the surrounding tissues was dropped a small portion of a one per cent. solution of osmic acid. This hardening agent fixed the undisturbed tissue, and made possible a later removal and further fixation of it. After this preliminary fixation of from fifteen to thirty minutes the tissues were carefully lifted into a capsule containing one per cent. osmic acid solution and the capsule placed in a darkened chamber for twenty-four hours. After the expiration of this period and an additional three hours of washing in distilled water, the material was carried through increasing percentages of alcohol, cleared in xylol and embedded in paraffin.

The sections were cut in ribbons by a MINOT microtome to a thickness of three and one-third micra, and, after being spread by gentle heat, were fastened to the slides with albumen fixative. Thorough drying was followed by a second clearing in xylol, after which the sections were mounted in colophonium under thin cover glasses.

a. Enumeration. The fibers in the sections of the main trunks were enumerated by the "photographic method" which has been used and described by Dr. HARDESTY, 1899.

For the thigh and shank branches the "net method" was adopted.

In the employment of either method special effort was made to include the very small medullated fibers which, under ordinary circumstances, elude observation.

b. *Determination of average areas for¹ each fiber.* The determination of areas was made by the aid of camera lucida drawings of the selected sections. In the execution of these drawings all of the nerve sheath was excluded and the outline was made to follow the periphery of the nerve fibers, thus including only the fibers themselves and the spaces lying between them. The area included by the outline of this camera drawing was determined by planimetric measurement and the diameter by a millimeter scale. The accuracy of this diameter measurement was tested by actual measurement upon the section itself. From these data the true area of the section was computed.

The average area for each nerve fiber was determined by dividing this true area expressed in square micra by the number of fibers contained in the section.

For any section in which spreading had occurred, the percentage of added space was determined by a special method. The section was photographed and on the print the additional space was lightly outlined in pencil. By carrying the planimeter along the pencil line the added area was measured. The portion of the entire area of the photographed nerve which this included area covered gave the percentage to be deducted from the former computed area of the nerve.

c. *Determination of the average area of the largest fibers.* Confirmatory measurements were made upon the largest fibers at the several levels. For each of these fibers the mean of two diameters was obtained, and from this mean the area of the selected fibers was computed.

¹ The area *for* the fiber is an average area determined by dividing the area of the nerve trunk by the number of nerve fibers of which it is composed, while the area *of* the fiber is determined by measurements made upon the fiber alone. The distinction made in this and the following section between the area *for* the fiber and the area *of* the fiber is maintained throughout the discussion, and the italicised words require this difference in interpretation wherever they are introduced.

The number of fibers selected at each level varied according to the proportion of fibers present at that level. In measuring the largest fibers in the branches, a number of fibers equal to the number of fibers measured at a level just above the branches was selected and their average area computed. A second computation for the proportional number of fibers in the branches was then undertaken. Both results are included in the tables.

B. Number of Nerve Fibers.

- I. Enumerations at the various levels of the sciatic and crural nerves, and of the thigh and shank branches at their points of separation from the main trunks.

In ascertaining the number of nerve fibers at different levels for this frog, the first count was made at a point in the sciatic and crural nerves above their branches to the thigh, at the points C and S_1 , Figure 2. The next level selected was in the sciatic nerve immediately below its branches to the thigh, at S_2 . As the crural nerve sends all its fibers to the thigh tissues, the sum of the numbers at the first level gave the total number of fibers which innervate the thigh, shank and foot. That at the second level indicated the number passing on to the shank and foot, while the difference between the numbers at the two levels gave the calculated number of fibers innervating the thigh.

Reference to Table V gives the desired counts. The crural nerve for the left side supplies 1630 fibers, for the right side 1627 fibers, to the thigh. The sciatic nerve above its branches to the thigh shows for the left side 5499 fibers, for the right side 5480 fibers. This gives a total count of 7129 fibers for the left side, 7107 fibers for the right side. The number of fibers at S_2 , below the branches to the thigh is for the left side 3962 fibers, for the right side 3942 fibers. By process of subtraction the probable number of fibers innervating the thigh is found to be for the left side 3167 fibers, for the right side 3165 fibers.

TABLE V

Showing the calculated number of fibers innervating the thigh.

Frog II B.		L.	R.
Levels ¹			
C	Observed in crural nerve,	1630	1627
S ₁	Observed in sciatic nerve above its branches,	5499	5480
C+S ₁	Observed total to thigh, shank and foot,	7129	7107
S ₂	Observed in sciatic nerve below its branches to the thigh,	3962	3942
(C+S ₁)-S ₂	Calculated number innervating the thigh,	3167	3165

¹The designations of levels in this and the succeeding tables are those of Tables I or II, and Figures 1 and 2.

Table VI shows the actual number of nerve fibers by count passing to innervate the thigh. The number of fibers to the left side is 3481, to the right side 3508 fibers. These thigh fibers innervate on each side, the cutaneous covering of the thigh and twenty thigh muscles.

TABLE VI.

Showing the observed number of nerve fibers innervating the muscles and skin of the thigh.

Frog II B			
Designations of levels.	No. of muscles.	No. of fibers.	
		L.	R.
S ₂ and 3	1	398	407
S ₄ and 5	2	150	167
S ₆	8	852	846
S ₇	1	67	65
S ₈	2	311	318
S _{8x}	1	73	78
Sciatic nerve,	15	1851	1881
Crural nerve,	5	1630	1627
Totals	20	3481	3508

Table VII indicates the observed number of fibers to the shank and the number of muscles, six, which they innervate. The proportion of muscular to cutaneous fibers in the thigh and the shank will be discussed in another section. The ob-

served number of fibers to the shank, as shown in Table VII, is 2108 fibers for the left side, 2130 fibers for the right side.

TABLE VII

Showing the observed number of fibers innervating the muscles and skin of the shank.

Frog II B.

Levels.	No. of muscles.	L.	R.
T. α .	0	20	31
T. β .	1	322	26
T. 1. a.		147	142
T. 1. b.	0	260	347
T. 2. a.	0	126	125
T. 2. b.	1	136	134
P. a. α .	0	9	10
P. a. β .	0	8	8
P. b.	0	480	482
P. c.	1	42	46
P. d.	1	75	52
P. 1. a.	1	2	47
P. 2. a.		457	464
P. 2. b.	1	24	26
Total to shank	6	2108	2130

Table VIII contains the enumeration of the nerve fibers innervating the foot. The number here entered is the result of a count at the fourth level which corresponds with the ankle. The count shows 2486 fibers for the left side, 2497 fibers for the right side.

TABLE VIII.

Showing the observed number of fibers innervating the foot.

Frog II B.

Levels.	L.	R.
T. 1	480	529
T. 2	840	833
P. 1	821	802
P. 2	345	333
Total to foot	2486	2497

For the enumerations contained in Table IX the levels selected were two in number, the ones that have been described as the third and fourth levels. The third level sections the tibial and peroneal nerves just above their branches to the

shank. The fourth level cuts, at a point opposite the ankle, the four subdivisions of the tibial and peroneal nerves which supply the tissues of the foot. This level lies only slightly below the point at which the last branches to the shank are given off.

The total number of fibers at the third level is for the left side 4146 fibers, for the right side 4152 fibers. The total number of fibers at the fourth level is, as has been shown in Table VIII, for the left side 2486, for the right side 2497.

The total number at the third level less the total number at the fourth level gives the calculated number of fibers to the shank, which is 1660 for the left side, 1655 for the right side.

TABLE IX.

Showing the calculated number of nerve fibers innervating the shank.

Frog II B.

Levels.		L.	R.
P.	Observed in peroneal nerve above branches to shank.	1922	1873
T.	Observed in tibial nerve above branches to shank.	2224	2279
P.+T.	Total observed to shank and foot	4146	4152
P. 1+P. 2+ T. 1+T. 2	Observed to foot.	2486	2497
$(P+T) - (P_1+P_2+T_1+T_2)$	Calculated to shank.	1660	55

2. Significance of the excess of the observed over the calculated number of fibers to both thigh and shank.

A comparison of Tables V and VI, relating to the fibers innervating the thigh, with Tables VII and IX, relating to the fibers for the shank, reveals a surprising discrepancy between the observed and the calculated number of fibers in each instance.

Table X, exhibiting the differences for the thigh, shows for the left side an excess of 314 fibers or 9% of the number of fibers concerned in innervating the thigh, for the right side 343 fibers or nearly 10% of the observed number of fibers innervating the thigh.

In the preceding study, DUNN, 1900, p. 233, the excess was from 6 to 8% of the observed number of fibers to the thigh.

TABLE X.

Showing the excess of the observed over the calculated fibers innervating the thigh.

Frog II B.

	L.	R.
Observed to thigh.	3481	3508
Calculated to thigh.	3167	3165
Excess of observed over calculated.	314	343
Percentage excess.	9%	10%

Table XI, a similar table for the shank, shows for the left side an excess of 448 fibers or 21% of the observed number of fibers and for the right side 465 fibers or 22% of the number of fibers found in the shank branches close to their points of separation from the main trunks.

TABLE XI.

Showing the excess of the observed over the calculated fibers to the shank.

Frog II B.

	L.	R.
Observed to the shank	2108	2130
Calculated to the shank	1660	1665
Excess of observed over calculated	448	465
Percentage excess	21%	22%

This disparity between the observed and the calculated numbers to the thigh, existing in each of the three frogs on which observations have been made, can hardly be due to an error in counting. The probable explanation, as pointed out in the earlier discussion of this disparity, DUNN, 1900, p. 233, is that of a branching of certain of the nerve fibers at some point between the levels at which they were counted. In several experimental teasings a number of large fibers were found in the sciatic trunk dividing near the departure of the thigh branches.

Another point of interest is the greater percentage of dividing fibers present in the shank. Their presence is ex-

plained by the fact that the point of section for these fibers was much nearer to the periphery than that for the fibers to the thigh. As has been indicated earlier in this study, the branches to the shank are given off to single muscles or frequently several branches pass to one muscle, while in the thigh the larger branches furnish fibers to several muscles, in one instance, the *ramus profundus posterior*, to eight muscles.

3. Discussion of the increase in the number of fibers at successive levels.

Enumerations of the fibers at two levels other than those already mentioned were made that they might serve as controls to the results obtained at the levels just below the branches to the thigh and just above the branches to the shank. At no point between these four levels are nerve branches given off with the exception of a few very fine branches of four or five fibers each, which cannot be traced by fine dissection but seem to pass to surrounding tissues other than muscular tissue.

From the level in the sciatic nerve just below the thigh branches, indicated in Figure 2 by S_2 , through the levels indicated in the same figure by S_3 and T+P, to the level just above the branches to the shank, level T and P, the number of fibers shows a gradual increase. Reference to Table XII reveals the exact amount of this increase from one level to the next one. This increase must be due to fibers dividing in the main trunk.

TABLE XII.

Showing gradual increase in the number of fibers at successive levels between the separation of the last branch to the thigh and that of the first branch to the shank.

Frog II B.

Levels		L.	R.
S_2	In sciatic nerve at a level below branches to thigh.	3962	3942
S_3	In sciatic nerve above its division into peroneal and tibial.	3988	4083
T+P	In peroneal and tibial just after their separation.	3996	4103
T and P	In tibial and peroneal above branches to shank.	4146	4152

The average increase in number for the two sides shows for the distance S_2 to S_3 (see Figure 2) an increase of 85 fibers, for the distance from S_3 to T+P of 14 fibers, and from T+P to T and P of 100 fibers. While this increase in the number of fibers is not proportional to the distances between the various levels, nevertheless the shortest distance, S_1 to T+P, gives the least increase.

4. Proportion of the number of muscular to the number of cutaneous fibers.

The proportion of the number of muscular to the number of cutaneous fibers will be of more definite interest when further data concerning the weight of the muscles and the area of the skin innervated have been obtained. As, however, the cutaneous and the muscular fibers were distinguished in this series of enumerations the results are recorded.

Tables XIII and XIV give in detail the number of muscular and of cutaneous fibers for the thigh and for the shank. Table XIII gives as the totals for the thigh 1805 muscular, 1676 cutaneous fibers for the left side, 1830 muscular, 1678 cutaneous fibers for the right side. In this instance the muscular fibers, while surpassing in number the cutaneous fibers, are not so much in excess as in the two frogs which furnished the data for the preceding study (DUNN, 1900, pp. 233, 234). The proportional differences in the several frogs seem to be matters of individual variation.

TABLE XIII.

Showing the number of muscular and of cutaneous fibers innervating the thigh.

Frog II B. Levels.	Muscular.		Cutaneous.	
	L.	R.	L.	R.
$S_2 \& 3$	23	55	375	352
$S_4 \& 5$	150	167		
S_6	710	705	142	141
S_7	67	65		
S_8	311	318		
S_{8x}	73	78		
Sciatic.	1334	1388	517	493
Crural.	471	442	1159	1185
Totals.	1805	1830	1676	1678

Table XIV, for the shank, shows also a greater number of muscular than of cutaneous fibers. The absolute numbers are, for the left side, 1205 muscular, 903 cutaneous fibers, for the right side, 1127 muscular, 1003 cutaneous fibers. There are at present no data for comparison with this enumeration for the shank.

TABLE XIV.

Showing the number of muscular and of cutaneous fibers innervating the shank.

Frog II B. Levels.	Muscular.		Cutaneous.	
	L.	R.	L.	R.
T. α			20	31
T. β	322	216		
T. 1. a.	147	142		
T. 1. b.			260	347
T. 2. a.			126	125
T. 2. b.	136	134		
P. a. α			9*	10*
P. a. β			8*	8*
P. b.			480	482
P. c.	42	46		
P. d.	75	52		
P. 1. a.	2	47		
P. 2. a.	457	464		
P. 2. b.	24	26		
Totals.	1205	1127	903	1003

*Articular.

5. Comparison of the number of nerve fibers for the two sides.

Even the most casual examination of the tabulations already presented reveals a striking accordance between the number of fibers for the two sides. This confirms the previous observation. There appears however to be a slightly greater variation for the branches to the shank. This irregularity may be a matter of individual variation, or, if it be found present in other specimens, may be one of several irregularities of innervation which the shank seems to exhibit.

No interpretation of the uniformity in the number of fibers for the two sides seems called for. The fact of symmetry in the number of fibers is what might naturally be expected from the corresponding uniformity for the two sides of the mass of tissue innervated and from their physiological similarity.

C. Diameter of the Nerve Fibers.

1. Introduction.

We propose to consider at this point whether the destination of a nerve fiber in the frog's leg can be inferred from its caliber. The law of SCHWALBE (SCHWALBE 1882), to which reference has already been made, sets forth the view that the largest fibers run the longest distance. The researches upon which this theory is based were carried on some twenty years ago, having been published in 1882. SCHWALBE based his observations on a study of the dorsal and ventral roots of the spinal nerves in *Rana esculenta*. His technique consisted of macerating the entire nerve root in 20% nitric acid at 40° C, and washing once in a large amount of water, or of hardening and staining in 1% osmic acid for twenty-four hours, washing and macerating in glycerine, acidulated with 1% of hydrochloric acid commercial strength, for 24 hours at 40° C (DUNN, 1900, p. 13). The nerve tissue thus prepared was then teased, and transverse measurements were made of the selected fibers. The average number of measurements for each root was twenty (SCHWALBE, p. 11). From these measurements he constructs a table showing first the average thickness, and next the thickness of fibers of greatest frequency. Now, when the corresponding curves from the ventral and dorsal roots are plotted it appears that in the cervical region the fibers of the second nerve have the largest average diameter, and in the lumbar region those of the eighth nerve. Finding these largest fibers present in the roots distributed to the fore and the hind leg respectively, he asks the question on page twenty, "Was liegt nun aber näher, als die stärkeren Kaliber in den Wurzeln der Extremitätennerven mit der grösseren Länge der betreffenden Nervenstrecke in Zusammenhang zu bringen! Wollte man diese natürlichste Auffassung nicht acceptiren, so wüsste ich nur eine Möglichkeit der Deutung jener Unterschiede. Man könnte nämlich der Meinung sein, dass die Extremitätennerven häufiger innervirt würden, als die Nerven des Brust- und Bauchumfanges, und in Folge dieses häufigeren Gebrauches sich stärker entwickelt hätten."

As SCHWALBE finds no evidence that the nerves to the extremities are more frequently innervated than those to the thorax and abdomen he is by exclusion compelled to accept the first hypothesis. This he proceeds to test. In the three frogs chosen he finds the length of the brachial nerve to its extremity as compared to the length of the ischiadicus to be approximately 1:2.35 (SCHWALBE, 1882, p. 21); that is, if there were a direct relation, the ratio between the squares of the diameters of the nerve fibers in these localities should correspond to that for their length and be 1:2.35, but their ratio is much less, being in the most favorable case, 1:1.5.

Instead of admitting, therefore, that the relation does not hold, SCHWALBE prefers to assume that the general relation is true but is modified by some other factor. He assumes, then, that some other influence is working to render the caliber of the nerve fibers in the brachial nerve greater than it should be in proportion to the length of the nerve.

Moreover he emphasizes the fact (p. 24) that these remarks refer to the sections of the spinal nerves nearest the spinal cord and that in their further course these fibers are modified, that is to say, reduced in diameter.

He then proceeds to explain in accordance with his theory what must be the meaning of a nerve containing fibers differing greatly in diameter, and states that the smallest fibers must be given off in the branches nearest the spinal cord. It is to be noted that SCHWALBE has no observations to confirm this view.

During the course of the present study the attempt was made to ascertain the destination of the very large fibers in the sciatic nerve. To this end measurements of the nerve fibers were taken at the levels at which the fibers had been enumerated. These levels are shown in Figure 2 and fully explained in Section B, Number of Nerve Fibers, page 310.

These two lines of investigation were followed: first, a determination of the average area *for* each nerve fiber at the various levels; second, a determination of the absolute measurements *of* the largest nerve fibers at the same levels, and in the branches.

2. Average areas *for* the nerve fibers above and below the branches to the thigh and shank.

The average area *for* each nerve fiber at the selected levels is shown in Table XV.

TABLE XV.

Showing the average area *for* each nerve fiber of the sciatic and crural nerves and their subdivisions at the levels above and below the thigh branches and above and below the shank branches.

Frog II B.		L.	R.
S ₁ & C.	Sciatic and crural nerves above branches to thigh.	97.2 □ μ	87.2 □ μ
S ₁	Sciatic nerve above branches to thigh.	100.9	91.2
S ₂ .	Sciatic nerve below branches to thigh.	76.6	81.9
T. & P.	Tibial and peroneal nerves above branches to the shank.	62.2	62.6
P ₁ .T ₁ .	Tibial and peroneal nerves below branches		
P ₂ .T ₂ .	to shank.	51.5	52.3

Looking at the left side alone, the average area for each fiber above the branches to the thigh is 97.2 square micra, when the average of both the sciatic and crural nerves is taken, 100.9 square micra, when the attention is confined to the sciatic nerve alone. The computation for the crural nerve should be disregarded in the discussion of changing caliber, since the crural nerve sends all its fibers to the thigh and hence furnishes but the one level for measurement.

The comparison of the average area mentioned with the area of 76.6 square micra for each fiber at a level below the branches to the thigh, S₂, shows a considerable lessening in the average area for each nerve fiber. By comparing the average area above the shank branches, T & P, 62.2 square micra, with that below the shank branches T₁, T₂, P₁, P₂, 51.5 square micra, we find a similar if not proportionate lessening in the average area *for* each nerve fiber. We find then in both the thigh and the shank a greatly decreased average area at the level below the branches. This decrease is in part due to the absence at the second level, below the branches, of the largest fibers which appeared at the level above the branches,

and the departure of these large fibers to the thigh tissues, as we shall show by our measurements upon the largest fibers at the two levels and in the branches. A second factor influencing this decrease is the diminution in caliber in the course of the individual nerve fibers.

That the second factor is subsidiary to the first is shown by the fact that the distance between the first and second levels is a comparatively short one, while the decrease in average area is very marked. We proceed to discuss these factors in detail.

3. Average areas of the largest fibers at the various levels.

We have suggested that the largest fibers at a level above the branches to the thigh and shank respectively are not present at a level below the branches. To verify this observation and to ascertain absolutely the destination of these fibers, measurements were made of a selected number of the largest fibers at these levels and also in the branches themselves. The number to be measured at each level was made proportionate to the total number of fibers at that level.

Table XVI indicates for the sciatic nerve and its subdivisions, the number of fibers measured, the level, its designation, and the average area of the fibers expressed in square micra, while Table XVII records the measurements for the branches. The measurements recorded in Table XVI are for the levels above and below the branches to the thigh and the shank, and control measurements, as the third and fourth records, which were made at levels lying between the level below the thigh branches and that above the shank branches. In Table XVII two sets of measurements are recorded; the first is the average area of the number of fibers corresponding to that measured in the section at a level above the branches; the second shows the average of the number which correspond to the proportion which the number of fibers in the branches bears to the number in the trunk. The tabulated measurements are for the left side of Frog II B.

TABLE XVI.

Showing the average areas of the largest nerve fibers at the various levels of the sciatic nerve and its subdivisions at which the areas for the nerve fibers had been computed. The number of fibers measured at each level is proportionate to the entire number at that level.

No. of fibers	Nerve	Level selected	Designation	L.
22	Sciatic	Above br. to thigh.	S ₁	229.6□
16	Sciatic	Below br. to thigh.	S ₂	173.0
16	Sciatic	Above division into peroneal & tibial.	S ₃	167.4
16	Tibial & peroneal	At separation.	T+P	166.0
16	Tibial & peroneal	Above br. to shank.	T and P	164.7
10	Tibial & peroneal	Below branches to shank	T ₁ , T ₂ , P ₁ , P ₂	106.0

TABLE XVII.

Showing the average area of the largest fibers in the thigh and shank branches. The first computation in each instance is for the number of fibers corresponding to that measured at a level just above the separation of the branches. The smaller number of fibers is proportional to the total number in the branches.

No. of fibers.	Level selected	Averages areas
22	Branches to left thigh	212.8□μ.
8	Branches to left thigh	232.9
16	Branches to left shank	127.9
6	Branches to left shank	144.9

We have, then, in Table XVI, the average areas for the same relative number of fibers at various distances from the spinal cord. These largest fibers at each level are highly uniform in size and hence the average represents also the individual fiber.

If the largest fibers in the lumbo-sacral plexus run the longest distance, the largest fibers at the highest level should appear again and again with at least only slightly decreasing diameter at the successive levels. By reference to Table XVI, the largest fibers at S₁, and S₂, points separated by not more than one centimeter, do not show this equality, but reveal at the second level a marked diminution in the average area, one of 46.7 square micra or 20%. Conical diminution cannot

furnish an explanation for so marked a variation in diameter at these adjoining levels. We must consider the possibility of the disappearance from the second level of the largest fibers, and the consequent measurement at that point of a set of fibers of less though still large caliber. The largest fibers may have passed out by way of the thigh branches to supply the thigh tissues, so their presence in those branches must be determined. Reference to Table XVII shows that the average area of the twenty-two largest fibers in the branches approximates that of the twenty-two largest fibers at a level above the branches, while the measurements of the eight largest fibers in the branches, the number proportional to the total number of fibers in the branches, show an average slightly greater than that recorded for the largest fibers at the level above the branches.

With these measurements for our consideration, we can arrive at but one conclusion, namely, that the largest fibers of the lumbo-sacral plexus, formed from the VIIth, VIIIth, and IXth spinal nerves, pass off in the branches to the thigh and therefore run a comparatively short course to terminate in the tissues which lie above the knee.

Fixing our attention upon the results of the measurements below the knee, we find that the difference between the average areas above and below the shank branches is 58.6 square micra or 36%, a greater difference than exists in the thigh. At the same time we find that the distance between the levels at which the measurements were made is much greater than that between the corresponding levels in the thigh, so that conical diminution may here exert a more decided influence than in our results for the thigh.

Comparing for the shank the average area for the largest fibers in the trunks, Table XVI, with the average for the branches, Table XVII, we find that the average for the largest fibers at a level above the branches is nearly equal to the average for the largest fibers in the branches and is much larger than the average area for the largest fibers at the level just below the branches.

We find, then, from a study of Tables XVI and XVII,

that the area of the largest fibers at the ankle is less than one-half that of the largest fibers in the sciatic nerve above the level at which the first branches pass off to the thigh. While there may be present a conical diminution of the nerve fibers in their course, yet the actual presence of fibers in the branches equal in their area to the area of the largest fibers in the trunk above the branches, and the absence of fibers of equal diameter below the level of the branches seems to justify the definite statement that the largest fibers at each level of the sciatic nerve run the shorter course, while the largest fibers which innervate tissues more remote from the spinal cord are of less diameter.

4. Possibility of conical diminution in the extent of the nerve fiber.

Although the foregoing explanation seems the correct one for the great decrease in diameter when the largest fibers in a section above the branches are compared with the largest fibers in a section immediately below the branches, it is possible that conical diminution of the nerve fiber in its course may be present and exert some influence upon the results obtained.

By comparison of the averages for the measurements at successive levels between the first and last of which no fibers are given off, we obtain certain interesting results. The levels considered are those of S_1 , S_3 , T+P, and T and P, Table XVI. Measurements are here obtained at levels of more than four centimeters distance from S_1 , which show a gradual diminution in the average areas of the largest fibers at successive levels, with a total diminution, from the level below the branches to the thigh, to that above the branches to the shank, of 8.2 square micra.

This gradual, though slight, decrease seems to point to a confirmation of the theory of the conical diminution of the nerve fiber in its course.

STILLING (1869, pp. 931 to 935) in his classical researches upon the spinal cord, during the course of an historical and critical survey of the question of the decrease in diameter or the conical diminution of the nerve fiber, states that in the

white substance of the spinal cord certain fibers occur which decrease in diameter at lower levels. His conclusions, however, are vitiated, as are those of other of the earlier histological investigators, by the crudity of the technique of that period.

SCHWALBE, (1882, p. 40) in the paper already quoted touches upon the question of conical diminution in the peripheral nervous system. After referring to the findings of HENLE, KÖLLIKER and others, in which the smaller size of the motor and sensory nerve fibers near their terminations was recognized, SCHWALBE states the conclusions at which he had arrived from his own observations. These observations consisted of the measurement of fibers in the trunks of nerves destined for the muscles or the skin and again upon the corresponding fibers near their destinations.

His conclusion is in this sentence, p. 44: "Beide zeigen Verfeinerungen nach der Peripherie, die motorischen aber erst an der zahlreichen Theilfasern unter Querschnittszunahme der gesammten motorischen Nervenbahn; die sensiblen Fasern verschmälern sich dagegen schon vor der Theilung unter bedeutender Querschnittsabnahme der sensiblen Bahn!"

Of the later authorities KÖLLIKER, 1896, in his condensation of the subject of nerve fiber diameter states that some fibers are smaller near the nerve cell than at a greater distance and that certain fibers, notably the sensory fibers, diminish in diameter near the periphery. He reaches the conclusion that the entire subject of nerve fiber diameter has not been sufficiently worked over to make possible any definite statements regarding it.

Since, then, the observation of SCHWALBE regarding the lessening diameter of nerve fibers at the periphery is the only one based upon observations made upon fibers from mixed nerves between the joining of the spinal roots and the periphery, the present observations are offered in partial confirmation of the theory of conical diminution of peripheral nerve fibers in their course.

The special interest of these findings centers in the fact

that the diminution in the diameter of the fiber occurs in a large nerve trunk and at a considerable distance from any peripheral branches.

5. Area of the axis cylinder substance proportional to the area of the section.

In the discussion of the innervation of the various portions of the hind extremity of *Rana virescens* we have necessarily included both the medullary sheath and the axis cylinder in the determination of the average areas of the nerve fibers.

In attempting to eliminate as completely as possible all sources of error, there arose the question of a possible change from the normal proportion of the medullary sheath to the axis cylinder in these sections. Measurements were therefore made at the three chief levels to ascertain the existing proportion of the average area of the ten largest fibers at each level to the average area of their axis cylinders.

The results are embodied in Table XVIII.

TABLE XVIII.

Showing the average areas for the ten largest fibers and for their axis cylinders.

Frog II B. Left Side.	A.	B.	
Level selected.	Average area ten largest fibers.	Av. area of their axis cylinders.	Ratio B. to A.
Sciatic above branches	222.73 $\square \mu$	108.62 $\square \mu$	1:2.05
Sections at knee	130.69	62.49	1:2.09
Sections at ankle	89.20	43.01	1:2.07

Reference to this tabulation shows that at each of the three levels the average area of the axis cylinders of the ten fibers measured is approximately one-half that of the average areas of the entire fibers. Hence the 1:1 relation (DONALDSON, 1895) of the medullary sheath to the axis cylinder prevails here also.

The results at each level are so nearly uniform that we are justified in the conclusion that, in all the measurements, not only the areas of the entire fibers bear certain relations to one another, but that their most actively functional portions, the

axis cylinders, stand in the same relations—a fact that increases somewhat the value of this series of observations.

6. Comparison of the average areas *for* the fibers with those determined by previous measurements.

While the general relations of the results of these measurements are much the same as those obtained by earlier investigations, so far as the thigh is concerned, yet the resulting figures are considerably lower in value than those heretofore obtained. This may be due to one of several causes.

First, the proportion of fibers of various sizes may be differently adjusted in the various frogs. Concerning the numbers and proportions of the fibers of varying sizes in the peripheral nervous system we have no definite information. A fact that seems to negative the probability of changed proportions is the observation that the ten largest fibers at any level are in this series of observations less in diameter than the ten largest fibers at the same level in any previous series of observations.

Again, some change may have taken place in the individual nerve fibers during the process of preparation of the sections, but if a shrinkage of the fiber in its entirety had taken place the sections would exhibit increased spaces between the fibers. No such separation of fibers appears in these sections. Or, if the change were in the axis cylinder alone, or in the medullary sheath alone, the usual relation of 1:1 existing between the areas of these two portions would be lost.

Table XIX, showing the average areas of the nerve fibers and of their axis cylinders in Frog B of the first series and Frog B of the second series, shows but slight deviation in either frog from the usual 2:1 relation of the fiber to its axis cylinder or of the 1:1 relation between the axis cylinder and the medullary sheath. The smaller diameter of these ten fibers in Frog II B, the subject of the present study, is also shown in this table.

TABLE XIX.

Showing the average areas of the ten largest fibers and of their axis cylinders in Frog B and Frog II B.

Frog B. Sex. F. Weight 49.7 grams. Length 205 mm.
Frog II B. Sex. F. Weight 61.5 grams. Length 234 mm.

	A.	B.	
	Average area of fibers at level S ₁ .	Average area of their axis cylinders.	Ratio of B. to A.
Frog B.	290.13 $\square \mu$	156.14 $\square \mu$	1:1.85
Frog II B.	222.73	108.62	1:2.05

From these facts we seem justified in the conclusion that the relative smallness of the diameters of the fibers is a characteristic of this particular frog and is common to all the fibers.

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A NOTE ON THE SIGNIFICANCE OF THE SIZE OF NERVE FIBERS IN FISHES.¹

By C. JUDSON HERRICK.

The observations upon the relation between diameter and distribution of nerve fibers in the frog, reported upon by Miss DUNN ('02), call to mind certain facts which came under my notice in the prosecution of my researches on the nerve components of fishes and which may serve to supplement as well as to verify her observations.

The eye-muscle nerves of *Menidia* I have found (see Section 9 of the work cited in the appended bibliography) to contain both typical coarse motor fibers and also very fine fibers which leave the brain bound up in the same root with the others, but terminate peripherally on a different set of muscle fibers. All of the extrinsic eye-muscles have, in addition to the usual large muscle fibers, a large number of very small ones. These latter are, for the most part, segregated into a separate slip, which may have a slightly different origin from the main muscular mass. The finer nerve fibers can be separately followed from the superficial origin of the nerve to their insertion in the muscle and the separation of the finer muscle fibers from the coarse ones makes it easy to determine the exact distribution of the two kinds of nerve fibers. To quote from the work just cited (p. 389), "In the case of each of the six eye-muscles of which we have just been treating, the side along which the finer fibers of its nerve run contains much smaller muscle fibers than those which make up the body of the muscle, the diameter of these small muscle fibers often being no greater than that of a large nerve fiber. The smaller

¹Studies from the Neurological Laboratory of Denison University, No. XVI.

muscle fibers are not merely the ends of larger ones which have become attenuated near their insertion, but they run for nearly the whole length of the muscle, maintaining the same diameter and the same relation to the larger ones. They do not appear to differ from the ordinary fibers except in size, in their constant relation to the finer nerve fibers and particularly in the fact that they are in places more closely enveloped by a dense and very rich plexus of these finer nerve fibers and by a nucleated connective tissue interstitial substance."

The point in this description to which I here direct attention is the fact that the large and small nerve fibers leave the brain together and are apparently approximately equal in length. In fact, the smaller fibers in general may be a trifle longer, for they usually end farther out on the muscle towards its insertion than do the larger ones. The size of the nerve fibers is evidently correlated with the size of the muscle fibers to be innervated. I have verified this observation on several other bony fishes; viz., the cod, the gold fish and the cat fish, whose eye-muscles show the same peculiarity of innervation.

In Section 5 of the same memoir is described a similar condition in connection with certain muscles (presumably all of the visceral type) about the beginning of the oesophagus of *Menidia*. On page 264 the description of the innervation of the *m. pharyngeus transversus* is as follows: "This is a large stout muscle extending between the two inferior pharyngeal bones. It is incompletely divided into two parts, a large ventral part which is supplied by a small number of very coarse and heavily myelinated fibers, like those for the other branchial muscles which can be traced back into the common motor component [of the vagus nerve], and a smaller dorsal part which is dorsally confluent with the general constrictor muscles of the oesophagus and like them is supplied by many very fine fibers whose origin could not be traced. The muscular fibers of the ventral part are very large and thick, those of the dorsal part smaller, but not so small as those of the proper constrictor of the oesophagus." Here again we have a case where nerve fibers of the same length and type (both visceromotor) differ

conspicuously in diameter and this is correlated with a similar difference in the size of the muscle fibers innervated.

I have observed many similar cases, especially among the branchial muscles of fishes, whose fibers vary greatly in size, depending apparently upon the functional importance of the muscle in question. It is a general rule, though by no means an invariable one, that in the fishes large muscle fibers are supplied by large nerve fibers and conversely small muscle fibers by small nerve fibers, irrespective of the relative length of the nerve fibers.

Now, to return to Miss DUNN's paper, she finds that SCHWALBE's inference, that, other things being equal, the longest nerve fibers have the largest diameter, does not hold true in the case of the sciatic nerve of the frog. On the other hand, the largest nerve fibers, it appears from her observations, are given off with the branches for the thigh, while the shank and foot are innervated by the smaller fibers.

Now, if we confine our attention for the moment to the motor fibers of the sciatic nerve, those for the muscles of the thigh should be larger in diameter than those for the shank, provided our rule stated above holds true, since the muscles of the thigh are much larger and more important, functionally, than those of the shank.

But this peculiarity is not confined to motor fibers. In the study of the innervation of the cutaneous sense organs of fishes I have met with many analogous instances. Thus, the organs of the lateral line system of fishes are usually innervated by very large nerve fibers, the largest in the body. But in many fishes a part of the organs of this system are greatly reduced in size, and presumably in functional importance. That these reduced organs are of small functional importance is rendered still more probable by the fact that their essential sensory cells, the hair cells, exhibit a greater proportional reduction than the indifferent supporting cells. Now, these reduced organs, irrespective of their position on the body and hence of the length of the nerve fibers which innervate them,

are as a rule supplied by much smaller nerve fibers than are the large and highly functional organs of the same fish.

Still another case is furnished by the terminal buds (gustatory organs) of the outer skin and barblets of some fishes. The distribution and innervation of these organs I have worked out in some detail in the case of *Ameiurus melas*, as already reported (HERRICK, '01). These organs are similar in structure to the taste buds in the mouth and like them they are innervated by communis nerves, so that the nerves of the two sets of sense organs can be directly compared. It is characteristic of communis nerves generally that their diameter is less than that of other types of cerebro-spinal nerves and the medullary sheaths are thin. The communis nerves which supply the taste buds of the mouth cavity are not exceptions to this rule, but those which supply the very large gustatory organs of the outer skin of the siluroids are considerably larger and are provided with much more dense medullary sheaths than is usual for fibers belonging to this system. The more highly developed terminal organs and greater functional importance doubtless have called forth a change in the character of the nerve fibers. That these cutaneous sense organs of the siluroid fishes are in fact highly functional as a gustatory apparatus I can definitely affirm on the basis of experiments now nearly ready for publication.

Miss DUNN concludes that in the case which she has examined there is no direct correlation between the diameter of the nerve fibers and the length of the fibers. I would make this conclusion general and add to it that there is, in some cases at least, a correlation between the diameter of the fiber and the functional importance of the fiber, or the physiological importance of its terminal organ as compared with other organs of the same system. The qualification stated, "of the same system," is important. In 1899 I formulated (p. 173 of the *Menidia* paper) the following definition of the functional system of nerves: "Each system may be defined as the sum of all fibers in the body which possess certain physiological and morphological characters in common, so that they may react in

a common mode. Morphologically, each system is defined by the terminal relations of its fibers—by the organs to which they are related peripherally and by the centers in which the fibers arise or terminate." It so happens that throughout the vertebrate series the peripheral fibers of each system have certain tolerably uniform characteristics of caliber, medullation, etc., by which they may be distinguished from those of other systems. This fact lies at the basis of much of the recent work on nerve components, in the course of which the several systems of components have been followed through serial sections from their primary centers within the brain to their peripheral termini. These fiber characteristics are, however, by no means inflexibly fixed, but, as we have seen above, are sometimes subject to wide and very confusing variations, partly explicable as functional adaptations, partly as yet unexplained.

These variations oppose very grave obstacles to the determination of the morphological rank of any organs on the basis merely of the size of the nerve fibers innervating them. For instance, the division of the body musculature into somatic and visceral systems needs a much more secure foundation than that afforded by studies on the caliber of the nerve fibers supplying the several muscles such as have been made by GASKELL, SHORE, EDGEWORTH and others. This character is doubtless an important aid, but it requires rigid embryological control. This is clearly appreciated by some of these authors, who have followed their measurements of nerve fibers by an embryological study of the muscles innervated.

By way of summary, then, we conclude that each functional system of peripheral nerves has tolerably definite fiber characteristics, the basis for which is as yet unknown; that these characteristics are by no means invariable, but that the fibers of a given system may show considerable differences in caliber and medullation in a single animal; and that some of these differences, at least, may be correlated with the degree of functional development of the peripheral end-organ. In general, highly developed muscle fibers, sense organs, etc. receive larger

nerve fibers than similar organs in a state of structural and functional degradation.

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THE EYE OF THE COMMON MOLE, *SCALOPS AQUATICUS MACHRINUS*.

By JAMES ROLLIN SLONAKER, Ph. D.

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With Plates XVIII to XX.

Introduction.

During recent years a number of investigations have been made on degenerate and rudimentary eyes. Among the most important investigators may be mentioned: HEAPE (3), KOHL (4), RITTER (5), RABL (6), HAMANN (7), RETZIUS (8), LANKESTER (9), EIGENMANN (10), FORBES (11), PACKARD (12), and CUNNINGHAM (13).

The first four named have made important studies on the eye of the European mole (*Talpa europæa*). So far as I know the eye of the common American mole (*Scalops aquaticus*) has not been studied. Four varieties of this species have been described by TRUE (1). It is the common mole, or variety *machrinus* that I speak of in this paper.

Though there is a great similarity existing between the eye of *Scalops aquaticus machrinus* and the description of *Talpa europæa* as given by the above mentioned authors, I find some important differences. These will be mentioned later.

General Appearance.

The head of the mole is conical in shape, the nose or snout forming the apex. The fur gives it a regular contour. So dense and fine is the fur that it wholly conceals the ears and eyes. These may be seen, however, if one parts the hairs at the proper places. The position of the eyes may be readily seen if the hair is closely shaved from the head. When this is done the eyes appear as dark areas, almost one millimeter in

diameter situated well forward on the sides of the head. They lie imbedded in the muscular and fatty tissues completely beneath the skin. A small, almost circular, funnel-like depression marks the position of the eye cleft. It is impossible to open this cleft sufficiently to see the eye. The general external appearance after the removal of the hairs is seen in Fig. 1, Plate XVIII. This shows the position of the eye as seen from the side. It shows also the presence of a rudimentary concha. Some authors have claimed that an external ear is not present in the mole. It cannot be seen when the fur is on, but the ring-like cartilage can be readily felt.

The relative position of the eye to the skull is shown in Figs. 2 and 3. It is readily seen that the eye is no longer confined within the bony socket as in most mammals. It is protected in no way by a bony frame-work and is very closely associated with the skin. In fact, in removing the skin from the head unless one is especially careful, the eye is also removed.

After the removal of the integument in front of the eye it appears as a small black sphere about 1 mm. in diameter. Generally a lighter area can be seen in the anterior portion of the eye which marks the extent of the cornea. In the fresh condition the shape of the eye is almost spherical. In the hardened specimens, however, the contour often varies from regular to very irregular (Plate XIX). This depends largely on the kind of hardening fluid used.

Methods.

Most of the specimens were caught alive and killed with chloroform and ether. Immediately after death the eyes were subjected to the various hardening fluids. In some cases the eye was preserved in situ, in which case orientation was maintained by attaching a small tag to a definite part of the skin. In some other cases the whole head was hardened in order to show the relative position of the eye. In most cases the eye was isolated from the surrounding tissue. The orientation was then preserved by sticking the eye on a small piece of paper to which it remained attached until it was ready to be imbedded.

After imbedding in paraffin sections were made 5, 10 and 15 micra thick.

Several fixing agents were used, but those which proved most valuable were PERENYI's fluid, Potassium bichromate and 10% Formalin. Saturated solution of Bichloride of Mercury, 10% Nitric Acid, Absolute Alcohol, 50% Alcohol and Platino-aceto-osmic mixture were used with poor success. PERENYI's fluid usually preserved the eye in the best general shape, but is not good for the finer histological study. 10% formalin or potassium bichromate gave much better histological preparations. The latter, however, generally caused the retina to separate from the choroid and pigment layers.

Staining was done wholly on the slide. The following stains were used with good success. EHRLICH-BIONDI, WEIGERT, MINOT'S (23) Haematoxylin Method, Haematoxylin and Eosin, and Haemalum.

All the figures are semi-diagrammatic camera drawings. The outlines and the principal structures were sketched with the aid of the camera.

Stages Investigated.

Owing to the difficulty of procuring the embryos I have succeeded in studying but two stages in the development of the mole's eye: (1) The eye of the young at birth; and (2) the eye of the adult. Very little difference is noticed between the young and the adult. The most marked difference is a slight increase in size. The different conditions I will describe in detail later.

The difficulties which present themselves in obtaining material for the embryonic stages are not at first appreciated. As is well known, the mole hibernates late in the fall and spends its winter in nests and burrows from two to three feet below the ground. This depth is always below the region of frost and would thus vary in different localities.

In southern Indiana the young are born some time in March, generally before the adults come to the surface. One adult female containing three young was caught on the third of

March. This was after a week of warm rainy weather and the ground had completely thawed out. These young averaged 42 mm. in length.¹ A litter of four young just born were by chance dug up on the 21st of March of another year. These also averaged 42 mm. in length. I therefore conclude that these two sets of young were of practically the same age.

Making use of SUTHERLAND'S (2) formula, $T = M_1 \sqrt[6]{W}$, to determine the period of gestation we can approximate the time of mating. T is the gestation period in days. M is a constant for the order or family. For Insectivora it equals 25. And W is the average weight of the adult in pounds. The adult averages about .375 pounds. Hence we have

$T = 25 \sqrt[6]{.375}$, or T equals 21, the number of days of gestation.

Mating then occurs early in February, at least a month before the adults generally come to the surface. Two or three males have been caught running over the snow early in February which would indicate that this was a period of activity on their part at least. Since one cannot locate accurately their winter homes, it is practically impossible to catch the adult females until they come to the surface in March, too late to get the embryonic stages. Keeping the adults in confinement has not met with success. Conditions for their normal activities could not be easily provided, as they are rapacious feeders and require a considerable range.

The early stages of the development of the eye of the European mole (*Talpa europaea*) have been described by HEAPE (3). He says that the beginning of the unfolding which later forms the optic stalk is seen in an embryo 1.82 mm. long and at a time before the medullary groove has closed at any point. They appear as two lateral depressions in the floor of the anterior part of the medullary groove. In an embryo 2.33 mm. long the medullary groove is practically closed in front, but is still open behind. The optic vesicles are easily seen projecting outward, backward and downward from

¹The length in this case means from the tip of the nose.

the anterior end of the neural tube. The optic vesicles continue to increase in a normal way until the embryo has reached a length of about 3 mm. His further description is as follows: "It is interesting to note that for a considerable period after this stage the optic vesicles show but very slight advancement to the condition then attained; their growth appears now to be retarded in as marked a degree as it was advanced in the early stages . . . the sudden checking of the development in the mole we may expect is due to the specialization of this species. Any modification of an important sensory organ would doubtless rapidly affect the development of the organ, but such an extended modification as is apparent here says much for the primitive nature of the habits of the animal."

We thus see that in the development of the eye of this species there is a very early departure from the normal development. It is therefore not surprising to find the eye of the young at birth rather poorly developed compared with the advancement found in most mammals at the same period.

The conditions found in the eye of the adult European mole and our common mole are so similar as to warrant one predicting that the early embryonic stages would be also much alike.

The Eye at Birth.

The eye is easily seen as a small dark area beneath the skin. The integument separating it from the outside, which corresponds to the eye lids, is 31 mm. thick. The eye lids have fused together in such a manner as to leave only a small cylindrical opening (Figs. 4 and 8, *cl*). This opening is so small that it is not perceived by the unaided eye. It is therefore very doubtful if light ever enters it. The cleft also meets the eye at such an angle as to preclude all possibility of light entering along the axis of vision. Exteriorly this cleft appears as a slight funnel-like depression with a small darker center. I have been unable to open it sufficiently to see the eye from the outside. In cross section of the head one is impressed by the small size of the eye. It has an average equatorial diameter

of .55 mm. and an axial diameter of .57 mm. This corresponds very closely with the dimensions of the eye of the European mole at the same age. KOHL gives these diameters as about .55 mm. and .61 mm. respectively.

The shape of the eye is generally that of a sphere, though it may be distorted in many ways. This is very likely due to the action of the hardening solutions.

From sections through the eye and the entire head one at once sees that the position of the eye is different from most mammals. It is not confined within a bony socket nor in any way protected by a bony frame-work. The nearest it approaches the skull is about .4 mm. That part of the skull to which the extrinsic eye muscles are attached and through which the optic nerve passes is 3.5 mm. from the eye. It thus lies imbedded in the integument just beneath the skin, quite a distance from the normal position found in most mammals.

The aqueous chamber is absent and the vitreous chamber is seldom found. The entire space within the sclerotic is filled by the lens and the retina. Occasionally, however, in the region of the optic nerve a small remnant of the vitreous chamber still persists. In this respect the common mole differs widely from the description of this stage of the European mole as given by KOHL (4). He finds well developed aqueous and vitreous chambers.

The eye muscles are present and can be traced back a distance of about 3.5 mm. where they are attached to the skull.

The optic nerve of the young mole at birth presents some interesting conditions. It can be easily followed along the course of the eye muscles until it penetrates the skull in the neighborhood of the attachment of the muscles. Many of the nerve fibers at this age extend only a short distance beyond their exit from the eye ball. The optic tract, however, can easily be traced because its course is marked by the cells of the optic stalk. These cells are more or less inclosed by the nerve fibers which extend to the brain. As the fibers leave the bulb,

some of them go between these cells; but a greater number run parallel and external to them (Fig. 34 and 35). These cells in the optic tract resemble closely the ganglion cells of the retina which have not developed axonic or dendritic processes. They are, however, much shrunken and somewhat irregular in contour. Their size compares favorably with that of the cells of the inner nuclear layer. These cells of the optic stalk can be traced into the eye where they are more or less scattered and separated by nerve fibers and typical ganglion cells. Within the eye most of these cells lie with their long axes parallel to the nerve fibers, but outside they are arranged with the longest axis transverse to the course of the nerve fibers. The original cells of the optic stalk thus form a core around which the greater number of fibers are arranged. A few fibers, however, run between the cells.

A similar condition is found to obtain in other animals. STUDNICKA (14) says, "In *Petromyzon* the lumen of the stalk soon disappears, but its cells, or their descendants, persist throughout life as an axial core of glia cells in the nerve." In *Protopterus* he finds a similar condition, but the cells are fewer and more scattered. In *Necturus* he found that the lumen of the optic stalk persisted throughout life. He also says that in other *Amphibia* there is either an axial mass of glia cells or many similar columns scattered through the cross section of the nerve, and that this is the condition generally found in the higher vertebrates.

In the European mole KOHL finds in the embryo 8.5 mm. long that the fibers of the optic nerve just after leaving the eye lie in the groove of the optic stalk (choroid fissure) and that some of them later enter the lumen of the stalk. The greater number lie outside. At this age none of the fibers extend to the brain.

This agrees with ASSHETON's results (15) on the frog. He says, "The optic nerve is developed independently of the optic stalk, and at first entirely outside of it; but on the breaking down of the stalk some of the nerve fibers grow in between the cells."

HIS (16) and FRORIEP (17) and others do not agree with this. They say that the optic fibers follow the lumen of the optic stalk in their development from the retina to the brain.

ROBINSON (18) studied the relation of the optic nerve to the optic stalk in mammals and confirms the results of W. MÜLLER, KÖLLIKER, CAJAL, HIS and FRORIEP and says that the nerve fibers grow inside of the optic stalk and among the cells which constitute its walls.

The conditions which I have found in the young at birth indicate that the nerve fibers have grown between and around the cells of the optic stalk.

According to KOHL the optic nerve of the European mole has as good a development in the 12 or 15 mm. embryo as the one I have studied has at birth.

As the nerve fibers leave the eye-ball a great many are seen to decussate. This condition is found in both horizontal and vertical sections. That is, fibers from one side of the retina pass over to the opposite side of the optic nerve and vice versa. Some of them, however, remain on the same side of the optic nerve as that of the retina from which they originate. This relation has been described by KOHL in the mole and by CAJAL (19) and NICATI (21) in other vertebrates.

The lens at this stage is found to be quite regular in shape and almost uniform in size (Fig. 4 and 6). Its shape corresponds very closely to that of the lens of any mammal at birth. The average axial diameter is .019 mm. and transverse diameter .024 mm. The ratio of the axial diameter of the lens to the axial diameter of the eye is 1:30.

In structure the lens differs widely from that of a normal mammalian lens. It is composed of cells so crowded together and possessing such large nuclei that they resemble cartilage cells (Fig. 22, Plate XIX). Nothing is present which resembles normal lens cells. The shape of these cells is very irregular as can be seen in Fig. 22. When examined with a high power they show irregular processes extending in various directions. Frequently vacuoles are found within the cell. Figure 29 is a camera drawing of lens cells from an adult eye. The

conditions found in the young at birth are very similar to those here represented. By careful examination a single layer of cells may be seen extending over the anterior surface. These cells no doubt correspond to the layer normally present in the development of all vertebrate eyes. These cells are very much smaller than those composing the posterior and larger part of the lens. One can safely say that such a structure could not function as a normal lens.

In the development of the lens of the European mole KOHL finds that it proceeds in a normal manner, that at birth the cells of the posterior part of the lens capsule has elongated and almost completely filled the capsule. These cells appear at this stage as typical elongated lens cells with very distinct and large nuclei. I have not succeeded in finding such an arrangement in the young of the common mole even though sections were made in various planes of the eye. There is, therefore, a very great difference in these two species at birth. The lens of the common mole seems much more degenerate. Owing to the lack of material with which to study the embryonic stages, I am unable to say just how this degenerate condition has been reached. Two theories may be given: (1) after the lens has developed in a normal way the cells have been reduced to the condition found in Fig. 22; or, and this seems to me the most probable, (2) instead of the cells of the posterior part of the capsule elongating and developing into typical lens cells, they have simply increased in size and number. At a later date I trust I may be able to procure material and to clear up this matter. RITTER (5) favors the latter hypothesis.

The choroid and pigment layers are so densely pigmented that it is almost impossible to distinguish the boundary between them. These layers extend forward to the lens, where they end in the region of the ciliary muscles. Sometimes a slight projection can be perceived extending forward (Fig. 7) which is all that is to be seen of the iris. The iris at this age is generally absent and the pupil is as large in diameter as the transverse diameter of the lens. This condition also indicates that

the light no longer enters the eye, or at best only in a very obscure way.

The retina at this age practically fills the whole of the vitreous chamber. In sections of the eye the retina is frequently found more or less separated from the pigment and choroid layers. This is an abnormal condition and due to the action of the hardening fluids. Sometimes in the region of the entrance of the optic nerve a small space is observed which is the remnant of the vitreous chamber.

The principal layers of the retina are generally easily discerned, but owing to the apparent shrunken condition of the sclerotic the cells composing these layers are very much crowded. This is especially true of the ganglion cells.

All the elements of the retina at this age have been observed, with the possible exception of the rods and cones. I have not been able to demonstrate them with certainty in any of the specimens I have examined. The processes of the pigment cells are easily seen in places and might be mistaken for rods and cones. If they are present, they are in a much more rudimentary condition than that described by KOHL in the European mole of this age. He describes them as easily seen and about half as long as those in the adult. The immature development of the processes of the outer nuclear cells leads me to say that the rods and cones have not developed at birth.

The outer nuclei present an immature condition. They appear as elliptical cells and measure on an average .0036 mm. by .0100 mm. (Fig. 40). Processes are observed to start from these cells, but I have been unable to trace them any great distance. In no case have I been able to follow them into an enlargement which might be considered a developing rod or cone. The fault may lie in the method of staining. These cells form a well defined layer about five cells deep which averages .0225 mm. in thickness. It forms a continuous layer from the lens on one side around to the lens on the other. In the region of the lens these cells are not sharply separated by the outer molecular layer from those of the inner nuclear

layer. These two nuclear layers here seem to fuse. In other places they are separated by an extremely narrow but well defined outer molecular layer. It appears more like a line than a layer.

The cells of the inner nuclear layer are much more immature than those just described. They appear as irregular, rounded bodies of various sizes (Fig. 39). The average dimensions are .0039 and .0044 mm. These cells form a continuous layer which is about six cells deep and averages .0292 mm. in thickness. As stated above it is separated from the outer nuclear layer by the very narrow outer molecular layer excepting in the region of the lens where the two nuclear layers appear to fuse. I have been unable to find any processes in these cells in the specimens which have been examined. They thus present a much more rudimentary condition than the same elements in the European mole. KOHL describes the latter as possessing well defined processes and in general very similar to the condition found in the adult.

The inner nuclear layer is separated from the ganglion cell by the fairly wide inner molecular layer. This layer is not of uniform thickness. Owing to the very much crowded condition of the ganglion cells these cells may be found variously located throughout the molecular layer. Often the inner nuclear layer and the layer of ganglion cells are in direct contact, the inner molecular layer having been pushed aside.

The position and arrangement of the ganglion cells are quite varied. At times they will form a layer several cells deep, then again they will be crowded into a mass. In no case have I found them arranged in the manner found in the normal mammalian eye. They show a marked degree of development. All the ganglion cells possess a distinct nucleus and well defined nucleolus. Their average dimension is .0057 by .0107 mm. On the basis of development these cells may be divided into three groups. This is a purely arbitrary division and is based on the development of cell processes. (1) A very few ganglion cells are found which possess axonic and dendritic processes (Fig. 38). In such cases the dendrites are short and

soon terminate. The axones, however, can frequently be traced a considerable distance toward the exit of the optic nerve. This type of ganglion cell is the most mature and the largest of any found at this age. (2) A second type and by far the most numerous is represented in Fig. 36. It consists of a well rounded cell with but a single process. This process is the axone and can frequently be traced until it is lost among the other axones forming the optic nerve. This observation accords with the results of HIS (20). He says that the axis cylinder processes are the first to form in "motor cells" and that the protoplasmic processes are formed considerably later. (3) The third type of ganglion cells is the most immature of any. It is slightly smaller than either of the other kinds and possesses neither axones nor dendrites (Fig. 37). They are found scattered throughout the ganglion cell layer and at this stage are almost as numerous as the second type. I may be mistaken in calling them ganglion cells, for cells similar to these are found in the adult. Furthermore, they correspond very closely in size and shape to the cells of the original optic stalk found in the optic nerve. They might thus be considered homologous with them. This agrees with CAJAL's results (22). He says that in the optic nerve, perhaps also in the nerve fiber layer of the retina of all vertebrates, spindle shaped cells are found more or less isolated between the nerve fibers. There is no doubt in my mind that some of these should be placed in the same category with the optic stalk cell. But, since the number of these cells which do not possess axones has decreased in the adult, we must assume that some of them do later develop axonic processes. These three kinds of ganglionic cells have no special grouping or location, but are found variously located throughout the region of the ganglion cell layer.

The nerve fibers do not form a layer. Each fiber passes from its cell of origin almost directly toward the exit of the optic nerve. Nerve fibers can thus be seen going in almost any direction through the ganglion cell layer. That is, a ganglion cell may be so orientated as to send the axone toward the

lens or in the opposite direction. All possible positions between these two extremes are found. This confusion or lack of order in the arrangement is no doubt due to the shrinking of the eye, or to the development of the retina more rapidly than the sclerotic coat.

The Eye of the Adult.

Owing to the dense fine fur the eye of the adult is seldom seen in a hasty examination. But when the fur is removed or parted at the right place a small dark area is easily perceived which marks the position of the eye. A minute darker point in the center of this dark area is the eye cleft. It is so small that with the naked eye one can locate it only with difficulty.

The conditions found in the adult are very similar to those described in the young at birth. The eyelids are fused together so completely that I was unable to open the cleft sufficiently to see the eye. The cleft meets the eye at such an angle (Fig. 16, 17) that should light enter it would not be along the axis of vision. There is a marked difference in this respect in the eye cleft of the European mole. It is described by KOHL as approaching the eye along the axis of vision. Light might thus enter it and pass into the eye in a normal manner. The thickness of the lids or integument over the eye is .31 mm.

When the integument is removed the eye appears as a small, black, rounded body, almost one millimeter in diameter. It approaches a sphere in shape, but is not nearly so constant in form as found in the young at birth. Many of the sections of the eye show these departures very distinctly (Plates XIX and XX). Doubtless some of this apparent distortion is due to the action of the reagents. Figures 11 and 12 show distortions which were no doubt caused by the killing fluid. These were hardened in 10% nitric acid.

The equatorial and axial dimensions of eyes preserved in different fluids used are shown in Table 1.

TABLE 1.
Diameters in millimeters of cross sections of eyes preserved in :

Perenyi's Fluid.			10% Formalin.			2% Potassium Bichromate.			10% Nitric Acid.			Sat. Sol. Bichloride of Mercury.		
Specimen	Eq'atorial	Axial	Specimen	Eq'atorial	Axial	Specimen	Eq'atorial	Axial	Specimen	Eq'atorial	Axial	Specimen	Eq'atorial	Axial
30	.6798	.8034	60	.8034	.7210	47	.6798	.8652	70	.7210	.6592	22	.9064	.9270
25	.7416	.8240	61	.7416	.8240	48	.8446	.9270	71	.7210	.7210	23	.8652	.9270
26	.7828	.8652	62	.6798	.7622	49	.8240	.9270						
27	.7622	.8446				50	.7828	.9476						
28	.6798	.7622				51	.8652	.9270						
29	.7004	.8240				52	.8652	.8446						
31	.7004	.7828												
32	.6592	.7622												
Averages	.7133	.8085		.7416	.7891		.8103	.9064		.7210	.6901		.8858	.9270

When these fluids are arranged in the order of their effect on the eye and based on the general averages of the dimensions in Table 1, they readily fall into the order shown in Table 2.

TABLE 2.

Hardening Fluids	Equatorial Diameter in mm.	Axial Diameter in mm.
10% Nitric Acid	.7210	.6901
Perenyi's Fluid	.7133	.8085
10% Formalin	.7416	.7891
2% Potassium Bichromate	.8103	.9064
Sat. Sol. Bichloride of Mercury	.8858	.9270
Total General Average	.7744	.8242

From this we see that 10% nitric acid causes the greatest amount of shrinking and consequent distortion; and that bichloride of mercury causes little or none. In fact the tissues appear as though they had been swollen. The latter, however, gave very poor histological preparations and was not often used. The differences in diameter may be partly due to individual variation. For example, in Table 1, under PERENYI'S fluid one sees that the equatorial diameter varies from .6592 mm. to .7828 mm. and the axial diameter from .7622 mm. to .8652 mm. Similar variations showing equally great range are seen in the specimens hardened in 2% potassium bichromate. The total averaged equatorial diameter is about .77 mm. and the axial diameter .82 mm. This is an increase of over .2 mm. in similar dimensions found at birth.

When these dimensions are compared with those of the adult European mole as given by KOHL, we notice that the common mole eye is smaller. The greatest equatorial diameter which KOHL found was .9137 mm. and the greatest axial diameter was 1.0350 mm. The smallest eye he tabulates had an equatorial diameter of .6034 mm. and an axial diameter of .6896 mm. I presume that in his cases the great range in size is probably due, partially at least, to the action of the different killing fluids used.

The aqueous and vitreous chambers are sometimes both

present, sometimes only one is seen, or in some cases neither is found. The aqueous chamber is more uniform in shape than the vitreous. This is no doubt due to the fact that the anterior surface of the lens is generally more uniform than the posterior surface and the cornea is less likely to change its shape than the retina. In this respect the common mole differs widely from the European mole. KOHL describes definite and uniform aqueous and vitreous chambers in *Talpa europæa* which very closely resemble the condition found in most mammals.

The extrinsic eye muscles are well developed and can be easily traced back to their insertion near the optic foramen.

The optic nerve maintains a normal position and at this stage is composed largely of nerve fibres. The nerve is very small and is difficult to follow in a gross dissection. It leaves the eye at quite an angle with the surface (Fig. 19, 23 and 27). It then makes two rather sharp bends which occur within .3 mm. from the eye. The remaining part of its course is almost straight to the optic foramen. The average diameter of the nerve at the lamina cribrosa is .045 mm. It then becomes rapidly enlarged until it reaches a diameter of .135 mm. This enlarged portion extends about .18 mm. from the eye-ball. It then rapidly decreases until it is .0675 mm. in diameter. It maintains this diameter from .41 mm. from the eye to the skull. In the region of the enlarged portion the original cells of the optic stalk, which were described in the young at birth, and the nerve fibers are much more loosely connected and arranged than in the remaining portion of the optic nerve. The increase in diameter of the nerve in this region is also due to the fact that the retinal artery enters it about .2 mm. from the eye and enters the eye along with the fibers.

In cross sections of the nerve one sees that the cells and nerve fibers are more or less separated into groups or bundles by septa. This condition has been described by STUDNICKA (14) in *Protopterus* and many other forms.

The blood supply to the eye is quite good. The large artery centralis seems out of proportion to the small size of the eye. It has apparently not been reduced in size at the same

rate as the eye. It enters the optic nerve about .2 mm. from the eye and passes forward between the nerve fibres until it reaches the posterior surface of the lens. Here it branches and spreads out over the posterior surface of the lens and over the surface of the retina. The finer branches penetrate the retina and ramify between the retinal elements as far out as the outer boundary of the inner nuclear layer.

The lens of the adult mole is in many respects similar to that of the young at birth. It, however, presents a marked difference in form and size. The shape is by no means constant. It varies so much that no two eyes are likely to have the same form of a lens even though they come from the same animal. The anterior surface is generally much more regular in contour than the posterior (Plates XIX and XX). The shape varies from an almost spherical lens as seen in Fig. 23 to the very irregular form as represented in Fig. 25. A regular form as shown in Figs. 13, 14 and 26 is the exception. The shape which is most common is that of a cone as seen in Figs. 15 and 18. In one adult I found that each eye had a very irregular and degenerate lens (Fig. 9 and 10). The lens cells filled only a portion of the lens capsule and formed a very irregular mass. In this case the degenerate condition could scarcely be attributed to a lack of development of the lens cells due to pressure or want of room.

In two other adult moles I found each lens peculiarly formed (Fig. 19, 20 and 21). In each of these the lens was almost divided into two unequal parts; a smaller anterior and a larger posterior part. The two parts were in close contact, the union being almost that of a plane. On close examination I found that these parts were not wholly separated, but were united by a small pedicel of cells (Fig. 20 and 21). These uniting cells were elongated and resembled typical lens cells more than any which I had found. The remaining cells, however, were very similar to the cartilage-like cells described in the young. I am unable to give a reason for this odd shape. I have found such a condition in only two animals out of probably one hundred which have been examined.

The size of the lens also varies as greatly as does its shape. With the exception of Figures 16 and 17, the sections of the whole eye represented on Plates XIX and XX pass in each case through the center of the lens. From these figures one can readily see that the lens varies in size from almost none as shown in Figs. 9, 18, 23, 24 and 25 to the very large lens represented in Fig. 26. The most degenerate condition which I have found is shown in Fig. 24. In this case it has almost disappeared.

The cell structure of the lens presents the same characteristic as described for the young. The cells are irregular in shape and possess no constant form (Fig. 29). A well defined nucleus and nucleolus are usually distinguished. One also frequently finds vacuoles of various sizes and shapes in the cell bodies. The cells lack any definite arrangement and seem to fit into each other in a very irregular manner. The concentric arrangement found in a normal lens is wholly wanting. Judging from the shape and the character and arrangement of the cells, one can safely predict that the lens is no longer capable of functioning in a normal manner. Light passing through it would appear as though coming through ground glass.

When this lens is compared with that of the European mole, a very wide difference is noticed. The American mole lens is much more degenerate. RITTER (5) says that in all the sections of the European mole which he has examined the lens shows the same characteristic form. He further says that the capsule of the normal lens and the mole lens is the same, the cells the same, the same fiber formation is present and the chemical structure is in all its parts the same as that of a normal lens. He also finds in the development of the frog lens a stage in which it offers some similarity to that of the mole. It is the time just before the nuclear formation when it presents a very marked form. "The epithelium of the anterior capsule is a massive one-celled epithelium, the mass of the lens consists of a neat figure of five or six rows of cells, if one simply wishes to judge from the above nuclei. But although the lens nucleus is still absent the legality is already shown in every

nucleus and every cell which leads to the concentric fiber formation. It is just the beginning of the nuclear formation, to which the first fibers are grouped. The cells are bent round, concave toward the middle. The cells extend in two opposite directions toward the front and back. In this state of development the frog lens shows a later development. The mole lens does not follow this procedure. In its complete freedom in the position of the cells there is also a great increase and flattening of the cells." In regard to the capability of the lens of *Talpa europæa* functioning as a normal lens RITTER says, "The concentric structure is lacking and there can exist no mathematical picture. The lens is transparent and allows the light to penetrate to the retina. The perception of light and dark could take place at the retina. The image of an object must consist of distorted lines and a knowledge of the object does not seem possible."

The choroid and pigment layers of the adult eye present the same general characteristics as described in the young. These two layers are so closely attached and so densely pigmented that it is almost impossible to determine the boundary of each. In specimens where it is possible to distinguish the boundary between the choroid and pigment layers the choroid has an average thickness of .0041 mm. and the pigment layer of .0251 mm. They have a combined average thickness of .0298 mm. This thickness is nearly uniform throughout their extent. In cross sections of the eye these layers are seen to run forward to the outer margin of the lens where they terminate abruptly (Figs. 13 and 14). A small portion which usually does not possess pigment is sometimes found projecting forward slightly over the front of the lens. This portion corresponds to the iris. Figure 13, *i* shows the most perfect development of the iris which I have found. One readily perceives that the size of the pupil is about the same as the equatorial diameter of the lens. One can see the processes of the pigment cells projecting into the rod and cone layer. These processes are more easily demonstrated in regions where the retina has separated from the pigment layer (Fig. 15).

The retina of the adult mole very closely resembles that of the young. In many cases it completely fills the vitreous chamber. In others a small vitreous chamber is found (Fig. 9, 10 and 13). In cross sections one frequently finds a space between the retina and the pigment layer (Fig. 18, *s*). This is an abnormal occurrence and was caused by the preserving fluids.

The different layers of the retina appear distinct and of almost uniform thickness. In many cases the ganglion cell and nerve fiber layers have been reduced to a mass occupying the center of the eye and immediately in contact with the lens (Fig. 14). These two layers are so confused that they are no longer distinguished as two distinct layers. When a vitreous chamber is present the ganglion cells and nerve fibers are spread out into a more or less uniform layer (Fig. 13). A transitional form between these two extremes is represented in Fig. 18. Here the pencil-like vitreous chamber prevents the inner surface of the ganglion cell and nerve fiber layers from uniting and thus forming a mass. This condition is no doubt brought about by the growth of the retina much more rapidly than the sclerotic coat. It is thus confined in a smaller space than in a normal eye and conforms to this space in a variety of foldings and arrangements. All the layers of the retina show this crowded condition to a greater or less extent.

All the elements of the normal mammalian retina are found in the eye of the adult. Owing to the crowded condition of the retina these elements are not arranged in a normal manner. It is my belief that if the adult mole retina were spread out over a surface bearing the same ratio to the size of the body as obtains in other mammals the retina would be similar to that of the normal animal. The mass and number of elements present seem to substantiate this belief. No measurements have been made to test the validity of this supposition.

The thickness of the retina varies with different individuals and with different hardening fluids. Table 3 gives the thickness of the retina and its layers when hardened in the

TABLE 3.
Thickness of Different Layers of the Retina Preserved in Different Fluids.
Dimensions are in micra.

Specimen No.	Perenyi's Fluid.										10% Formalin.				2% Potassium Bichromate.						10% Nitric Acid			Sat. Sol. Mercuric Chloride.			Total Avg.
	25	26	27	28	29	30	31	32	Avg.	60	61	62	Avg.	47	48	49	50	51	52	Avg.	71	70	Avg.	22	23	Avg.	
Pigment	28.0	27.5	28.0	32.0	32.0	16.0	24.0	20.0	26.0	31.5	22.5	27.0	27.0	27.0	18.0	36.0	22.5	13.5	22.5	23.3	31.5	27.0	29.2	18.0	22.5	20.2	25.1
Rods and Cones	8.0	8.5	8.0	8.0	8.0	8.0	8.0	8.3	8.1	9.0	6.0	9.0	8.0	9.0	22.5*	9.0	9.0	4.5	4.5	9.7	8.0	4.0	6.0	4.5	4.5	4.5	7.5
Outer Nuclear	28.0	24.0	24.0	36.0	24.0	12.0	32.0	28.0	26.0	40.5	31.5	31.5	34.5	45.0	22.5	36.0	31.5	27.0	31.5	32.2	36.0	40.5	38.9	40.5	45.0	42.8	34.6
Outer Molecular	8.0	8.0	8.0	8.0	8.0	5.5	8.0	8.0	7.7	13.5	4.5	4.5	7.5	22.5	9.0	13.5	9.0	4.5	9.0	11.3	4.0	9.0	6.5	4.5	13.5	9.0	8.4
Inner Nuclear	36.0	24.0	32.0	36.0	40.0	16.0	48.0	40.0	34.0	54.0	40.5	22.5	39.0	36.0	36.0	40.5	45.0	36.0	49.5	40.5	49.5	31.5	40.5	40.5	45.0	42.8	39.4
Inner Molecular	36.0	48.0	40.0	76.0	32.0	32.0	48.0	40.0	44.0	81.0	45.0	45.0	57.0	90.0	63.0	67.5	67.5	54.0	54.0	66.0	31.5	36.0	33.7	40.5	36.0	38.2	47.8
Ganglion Cells	36.0	160.0	160.0	200.0	120.0	92.0	140.0	140.0	137.0	112.5	144.0	135.0	130.5	225.0	135.0	135.0	67.5	180.0	234.0	170.2	54.0	54.0	54.0	160.0	112.5	136.2	125.6
Nerve Fiber	12.0						16.0	20.0									45.0										
Total Retina	192.0	300.0	300.0	396.0	264.0	181.5	324.0	304.0	282.8	442.0	294.0	274.5	308.5	454.5	306.0	337.5	297.0	319.5	405.0	353.2	214.5	202.0	208.5	308.5	279.0	293.7	288.4

* The pigment layer had separated from the rods and cones so that the complete length of the latter could be measured.

same fluids as shown in Table I. Measurements were made as nearly as possible along the axis of the eye.

From this tabulation we see that the hardening fluids have affected the retina very much as they did the whole eye. We also perceive that there is a very great individual variation. For example, the eyes which were hardened in PERENYI's fluid show a thickness of retina ranging from .192 mm. to .396 mm. A very slight difference in the arrangement of the retina will greatly alter its thickness. To illustrate: Figures 13 and 14 are specimens numbered 25 and 27 respectively and were hardened in PERENYI's fluid. As shown in Table III, the former has a retinal thickness of .192 mm. and the latter .300 mm. In each of these cases the distance along the axis of vision from the posterior surface of the lens to the pigment layer is practically the same. In Figure 14 this whole distance is occupied by the retina, while in Figure 13 the retina occupies only a part. Such slight variations in the arrangement of the retina may thus cause a great difference in its thickness. From Table III we see that the average thickness of the retina of the adult is .2884 mm. This is much thicker than KÖHL found the retina of *Talpa europaea*. He found the retina of the adult .1313 mm. thick. The ratio of the thickness of the retina to the axial diameter of the eye he represents as 1:7.49. In the American mole the ratio is 1:2.85. The retina of the European mole is not so crowded and lies in almost a normal manner.

The rod and cone layer is quite uniform. It has an average thickness of .0075 mm. This does not represent the length of these elements. Owing to the processes of the pigment cells more or less concealing the rods and cones, it is almost impossible to measure to their external ends. A part of the internal segments is all that is to be noticed.

When the rods and cones are isolated they present characteristics very similar to those of the normal mammalian eye. The rods are quite slender and elongated. They have a total average length of .0286 mm. The internal and external segments are readily distinguished (Fig. 30, *r*). The former has

an average length of .0178 mm. and an average diameter of .0007 mm. It is almost uniform in diameter from its base to the abrupt tapering into the thread-like external segment. The external segment has an average length of .0088 mm. It is very delicate and resembles a thread or line. It extends outward in a more or less wavy manner and is lost among the pigment cells. The base of the rods lies near the outer boundary of the outer nuclear layer. In fact the bases of the rods frequently lie between the nuclei. A delicate process extends from the base of the rod to its nucleus (*nn*). This process is of various lengths depending on the position of the nucleus within the nuclear layer.

The cones are more conspicuous than the rods. They have a total average length of .0178 mm. There is more variation in their length than in the rods. They are found to vary from .0143 mm. to .0220 mm. Like the rods, they can easily be divided into the broad internal segment and the thread-like external segment (Fig. 30, *c*). The former has an average length of .0107 mm. and the latter .0071 mm. The internal segment has a greater variation in length than the external segment. It varies from .0085 mm. to .0142 mm. This portion of the cone is more or less cone-shaped, the base being wide and in direct contact with its nucleus. The average diameter of the base is about .0021 mm. It tapers rapidly to a diameter of .0014 mm. which it maintains for a short distance. It then decreases rapidly in diameter to the thread-like external segment. The bases of the cones do not lie in the same level. This is due to the fact that their nuclei seem to have been pushed sometimes inward and sometimes outward from their natural position. Those cones whose nuclei are most deeply located in the outer nuclear layer are the longest. The shortest cones are associated with the nuclei lying farthest out. The result is that the external segments of all cones lie in almost the same level.

The rods and cones stain in a normal manner and in general closely resemble elements in the normal mammalian eye.

The nuclei of the outer nuclear layer very closely resemble

those of a normal eye (Fig. 33). They are large and are surrounded by a thin layer of protoplasm. This stains faintly. A nucleolus is easily demonstrated. The rod and cone nuclei have almost the same shape and size. Those for the rods are slightly longer. They have an average size of .0045 mm. by .0078 mm. The average size of the cone nuclei is .0040 mm. by .0064 mm. The cone nuclei lie near the outer boundary of this layer. In fact, as already described, many are found between the bases of the rods.

The nuclei of this layer are arranged five deep and form a continuous layer averaging .0346 mm. in thickness. The boundaries of this layer are very irregular. Some of the nuclei appear as though pushed out into the adjacent layers. The nuclei forming the first and second rows from the outside generally belong to the cones. The remaining three rows are the rod nuclei. In the region of the lens, corresponding closely to the ora serrata of the normal eye, the nuclei of this layer blend and mingle more or less with those of the inner nuclear layer. The outer molecular layer in this region is wanting. I have been able to follow branches from these nuclei which connect them with the rods, but have been unable to trace the ingoing branches far toward the molecular layer. By this I do not mean to imply that such branches are not present. My preparations were not preserved and stained in a manner to show them at their best.

The outer molecular layer has an average thickness of .0084 mm. throughout its extent. In the region of the lens, as already described, it is absent owing to the fusion of the two nuclear layers. This layer is more or less encroached upon by nuclei which appear to have been pushed out from the two adjacent nuclear layers. Owing to the method of staining I have been unable to demonstrate the finer structures of this layer.

The inner nuclear layer has an average thickness of .0394 mm. The nuclei are arranged five deep (Fig. 28) and fairly close together. The nucleus is rather small and has an average size of .0044 mm. by .0052 mm. A distinct nucleolus is usually seen (Fig. 32). The nucleus is surrounded by a rather

wide area of protoplasm. The average size of the cell is .0074 mm. by .0095 mm. I have not been able to demonstrate the processes of these cells. Slight projections of the protoplasm are found in places which indicate that some of these cells are in the process of forming branches. This layer, as in the young at birth, shows the most rudimentary condition of any of the cells of the retina.

The inner molecular layer is quite variable in thickness. Its uniformity depends on the arrangement of the ganglion cell layer. When these cells are not crowded into a mass the inner molecular layer is quite uniform in thickness (Figs. 11, 12 and 13). Frequently, however, the ganglion cells encroach on this layer and we find it of various thicknesses (Figs. 16 and 18). The average thickness of this layer is .0478 mm.

The ganglion cells have no definite arrangement. In some cases they form a fairly uniform layer (Figs. 11, 12, 13 and 18), in others they are massed, all evidence of a layer having been destroyed (Figs. 14, 19, 24, 25, 26 and 27). In a normal mammalian eye these cells are arranged in one or two irregular rows. But in the mole they are always in more than two rows. The ganglion cells and nerve fibers are so confused in their arrangement that at the best they are not distinguished as two layers. They form a combined average thickness of .1256 mm. Most of the cells have the shape of typical ganglion cells (Fig. 31). They possess two or more dendritic processes (Fig. 31, *d*), which can be followed some distance from their origin. Owing to the fact that they took the stain poorly I was unable to follow them far from the cell. A single axone is given off from each of these typical cells. It can be traced in almost a direct course to the center of the retina where it joins with others to form the optic nerve. In regard to the relative position of the ganglion cells and the course of the axones the mole presents a marked contrast to the normal arrangement. The ganglion cells are not always oriented so that the dendrites can go directly toward the inner molecular layer and the axone toward the inner surface of the retina as found in the normal eye. The orientation is frequently such that the den-

drites have to make a turn through as much as 90° to reach the inner molecular layer. The position of the cell is usually such, however, as to allow the axone to pass without much turning almost directly to the optic nerve. The optic nerve thus presents a very different appearance in regard to its origin from that in the normal eye. The axones from the ganglion cells at the inner surface of the retina unite to form the beginning of the optic nerve. This passes directly through the retina. In the course through the retina these axones, or fibers, are joined by others from cells more deeply situated. The optic nerve thus gradually increases in the number of its fibers until the complete number is attained at the lamina cribrosa (Fig. 23).

The ganglion cells have an average size of .0123 mm. by .0153 mm. They possess a large nucleus and a distinct nucleolus (Fig. 31, *n* and *nl*). The nucleus and nucleolus stain deeply, but the cytoplasm stains only faintly. Besides these typical ganglion cells, one occasionally finds cells having no processes and corresponding closely to this type found in the young at birth. It is possible that these may be homologous with similar shaped cells in the optic nerve.

The retina of the adult thus presents some very rudimentary conditions. The rod and cone layer, the outer nuclear and outer molecular layers approach very closely to the normal condition. The inner nuclear layer, not having the cell processes so well developed, presents a more rudimentary condition. The inner molecular layer, ganglion cell and nerve fiber layers differ in many respects from the normal mammalian type. The arrangement of the ganglion cells, the course of the nerve fibers and the mode of origin of the optic nerve are of especial interest.

The outermost layers of the retina are the most regular and normal in appearance. This regularity decreases as one approaches the inner surface of the retina and becomes most pronounced in the ganglion cell and nerve fiber layers.

Though the retina is abnormal and rudimentary in many respects, I think it would still be able to function, though very imperfectly, if other conditions were favorable. The character

of the lens, the lack of a vitreous chamber, the closed lids and the condensed condition of many of the retinal elements all signify that, at best, the adult mole can do no more than distinguish between light and darkness.

A few experiments on the living animal seem to substantiate this assertion. An adult was placed on a table in the direct sunlight. It always started in a forward direction regardless of its orientation with reference to the sun. It would maintain this direction until it came in contact with some obstacle. It would as often go directly toward the sun as away from it. Light therefore had very little effect as the stimulus was insufficient to cause a change in the direction of locomotion. Shearing the fur from in front of the eye did not modify the results. The mole is decidedly stereotropic and is not quiet so long as it is not under something. I found that it would just as readily crawl and remain under a pane of clean glass in bright sunlight as under a board in the shadow. My experiments lead me to conclude, therefore, that the eye of the common mole is quite incapable of being stimulated to such a degree as to cause any modification in the activities of the animal.

Summary.

The eye of the common mole appears as an inconspicuous dark area situated well forward on the side of the snout. It lies imbedded in the muscle beneath the skin.

When the eye of the common American mole is compared with that of the European mole it is found to be much more degenerate in all its parts than the latter.

The eye is degenerate and is no longer capable of functioning in distinct vision. The most noticeable changes which have occurred as contrasted with a normal mammalian eye are:—

1. The fusion of the lids, thus reducing the eye cleft to a microscopic tube which is probably incapable of functioning in a normal manner.
2. The great reduction in the relative size of the eye.
3. The much crowded condition of the retina as a result of the decrease in the size of the eye as a whole.

4. The noticeable reduction in the size, or the complete absence of the aqueous and vitreous chambers.

5. The varied modification in the shape and size of the lens. Also the peculiar cell structure of the lense.

All the structures of the normal mammalian eye are present in some form or other.

The two stages of the eye which were studied, the young at birth and the adult, show a great similarity. The most noticeable difference is in the size of the eye and in the development of the retina.

The eye muscles and the optic nerve are easily traced back to the skull. At birth the nerve presents in its course from the eye to the skull a peculiar arrangement. It is composed of numerous cells and a few fibers. In the adult the nerve fibers are much more numerous.

The eye cleft as seen in cross sections shows the same diameter in both vertical and horizontal sections. It meets the eye at such an angle that it is impossible for rays of light, should any enter, to pass into the eye along the axis of vision.

All the elements of the normal retina are present, but, owing to the much crowded condition, the ganglion cell layer is much increased in thickness.

The lens which is found in a great variety of shapes and sizes is composed of large irregular cells with distinct nuclei. It is therefore incapable of functioning as a normal lens.

Considering the degenerate conditions which exist, it is extremely doubtful whether the eye of the mole functions in any sense. At the best it can do no more than distinguish between light and darkness.

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EXPLANATION OF ABBREVIATIONS AND FIGURES.

With the exception of the first three figures, all drawings were made with the ZEISS microscope, using apochromatic objectives 2, 4 and 8 mm. and oculars 12 and 4. They were outlined and the most important details put in by means of a BAUSCH and LOMB camera lucida.

- a.*—aqueous chamber
ax.—axones
bv.—blood vessels
c.—cones
chr. p.—choroid and pigment layers
cl.—eye cleft
cn.—cone nuclei
c. op.—cells of optic nerve
cor.—cornea
d.—dendrites
e.—eye
gc.—ganglion cells
i.—iris
im.—inner molecular layer
in.—inner nuclear layer
l.—lens
lc.—lens cells
l. cp.—lens capsule
ll.—lower eye lid
msc.—eye muscles
n.—nucleus
nf.—nerve fibers
nl.—nucleolus
n. op.—optic nerve.
nr.—nucleus of rods
om.—outer molecular layer
on.—outer nuclear layer
r.—rods
r. c.—rod and cone layer
s.—space caused by separation of retina from pigment layer
scl.—sclerotic
sh.—sheath of optic nerve
sk.—skull
ul.—upper eyelid.
v.—vacuoles
vc.—vitreous chamber.

PLATE I.

Fig. 1. Lateral view of an adult head after the fur was removed to show the position of the eyes and the very much reduced external ear. $\times 1$.

Fig. 2. Lateral view of adult skull showing relative position of eye and socket. $\times 1$.

Fig. 3. Dorsal view of adult skull showing relative position of the eyes. $\times 1$.

Fig. 4. Vertical section through the head of a young mole at birth. The section passed through the center of the eye cleft and lens. $\times 13$.

Fig. 5. Horizontal section of the head of a young mole at birth passing through the eye tangentially and almost parallel to the eye muscles (*msc.*). In the different sections the optic nerve can be traced along these muscles to the skull. The arrow points anteriorly. $\times 13$.

Fig. 6. Horizontal section of the same head as *Fig. 1*. Section passed through the center of the lens (*l*). The different layers of the retina, portions of the eye muscles (*msc.*) and the optic nerve (*n. op.*) are easily discernable. The arrow points anteriorly. $\times 29$.

Fig. 7. Horizontal section of same head as *Fig. 5* passing through the optic nerve (*n. op.*). A short distance from the eye the nerve shows the peculiar granular appearance which is characteristic at this stage. The arrow points anteriorly. $\times 29$.

Fig. 8. Horizontal section of same head as *Fig. 5* passing through the eye cleft. The arrow points anteriorly. $\times 29$.

PLATE II.

Fig. 9. Horizontal section of right eye of adult hardened in PERENYI'S fluid. Section passes through the center of the lens and the exit of the optic

nerve (*n. op.*). A peculiar arrangement of the lens is seen in that the cells (*lc.*) only partly fill the lens capsule (*l. cp.*). $\times 29$.

Fig. 10. Vertical section of the left eye of the same animal as Fig. 9. Eye hardened in the same manner. The same characteristics are seen in the lens. $\times 29$.

Fig. 11. Vertical section through the center of the lens of an adult eye hardened in 10% nitric acid. It shows the characteristic folding and wrinkling due to this reagent. $\times 29$.

Fig. 12. Horizontal section through the center of the right eye of the same adult as shown in Fig. 11 and hardened in the same manner. $\times 29$.

Fig. 13. Horizontal section through the center of adult eye hardened in PERENYI's fluid. It shows all the structures of the eye to be almost normal. $\times 29$.

Fig. 14. Vertical section through the center of the lens of an adult eye hardened in PERENYI's fluid. Shows the complete absence of aqueous and vitreous chambers. $\times 29$.

Fig. 15. Horizontal section through the center of lens of adult eye hardened by 10% formalin in the skin. Shows a peculiar shape of the lens. $\times 29$.

Fig. 16. Horizontal section of same eye as Fig. 15, passing through the center of the eye cleft, but not through the center of the eye. In Figs. 15 and 16 the retina is seen to have separated from the pigment layer due to the action of the hardening fluid. $\times 29$.

Fig. 17. Horizontal section through the center of the eye cleft of adult eye hardened in the skin by 10% formalin. Section passes tangential to the eye ball. $\times 29$.

Fig. 18. Horizontal section through the center of the lens of the same adult eye as Fig. 17. Shows a very much reduced lens. $\times 29$.

Fig. 19. Horizontal section through the center of the lens and optic nerve of an adult eye hardened in PERENYI's fluid. The lens shows almost double, the two parts united by only a small part of the lens tissue. $\times 29$.

Fig. 20. The lens from Fig. 19 magnified to show the cells. Typical lens-like cells are seen passing from the posterior part to the anterior and thus connecting them. The remaining cells have the peculiar cartilage-like appearance. $\times 65$.

Fig. 21. Outline of the lens from the opposite eye of the same adult as Fig. 19. The same peculiarity is again seen as in Fig. 20. "a"—"x" marks the position of the axis of the eye. $\times 65$.

Fig. 22. The lens from Fig. 6 magnified to show the character of the cells (*lc.*) at birth. They present the same characteristic cartilage-like appearance as seen in Fig. 20. A—x marks the axis of vision and the arrow points anteriorly. A layer of cells one cell deep (*l*) can be distinguished covering the anterior part of the lens. The cells in the remainder of the lens (2), only a part of them being drawn, show no definite arrangement. $\times 115$.

PLATE III.

Fig. 23. Horizontal section through the center of the lens and exit of the optic nerve of the adult eye. The almost spherical lens is seen, also two

conspicuous retinal blood vessels (*bv*). The nerve fibers can be traced through a mass of ganglion cells almost to the lens. $\times 29$.

Fig. 24. Horizontal section through the center of the lens of adult eye hardened in 2% potassium bichromate. The lens is here very much reduced in size. $\times 29$.

Fig. 25. Vertical section through the center of the lens of opposite eye of the same adult as Fig. 24, eye hardened in same fluid. The lens is again seen to be very much reduced in size and the shape is very irregular. A number of blood vessels (*bv*.) are represented in the mass of ganglion cells. $\times 29$.

Fig. 26. Section through the center of the lens of an adult eye hardened in 2% potassium bichromate. This shows an extremely large lenticular shaped lens. $\times 29$.

Fig. 27. Section through the center of the lens of an adult eye hardened in 10% formalin.

Fig. 28. Section of the retina through the region *A-B* of Fig. 27 magnified to show the cells of the retina. $\times 150$.

Fig. 29. Lens cells of adult magnified to show vacuoles (*v*), nuclei (*n*) and nucleoli (*nl*). $\times 250$.

Fig. 30. Rods (*r*) and cones (*c*) and their nuclei (*rn* and *cn*) of an adult. The entire thickness of the outer nuclear layer is represented, the inner boundary being represented by the line *o-m*. Hardened in 10% formalin. $\times 700$.

Fig. 31. Ganglion cells of adult showing the dendritic (*d*) and axonic (*ax*) processes. These two cells are from different parts of the retina. $\times 700$.

Fig. 32. Cells of the inner nuclear layer. $\times 700$.

Fig. 33. Cells of the outer nuclear layer. $\times 700$.

Fig. 34. A portion of the optic nerve of the young at birth taken from the region where the line "*s*" crosses the nerve in Fig. 7. Magnified to show nerve fibers (*nf*) and the cells of the optic stalk. $\times 250$.

Fig. 35. A portion of the optic nerve of the young at birth from the region indicated by *C-D* of Fig. 34 more highly magnified. The nerve fibers (*nf*) and the cells of the optic stalk (*c. op.*) are seen more or less intermingling. $\times 700$.

Fig. 36. Ganglion cells of the young at birth showing the axonic process (*ax*) and the absence of dendrites.

Fig. 37. A group of ganglion cells from the retina at birth in which some are seen which have not yet produced axones.

Fig. 38. A typical ganglion cell from the retina of the young at birth. Such a cell is only occasionally found at this stage. The most common types are shown in Fig. 37. $\times 700$.

Fig. 39. Cells from the inner nuclear layer at birth. $\times 700$.

Fig. 40. Cells from the outer nuclear layer at birth. $\times 700$.

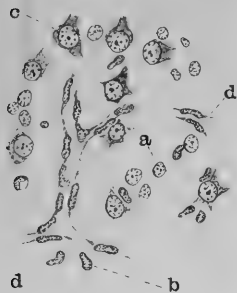


Fig. 1

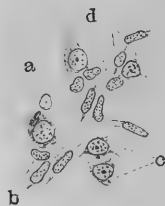


Fig. 2

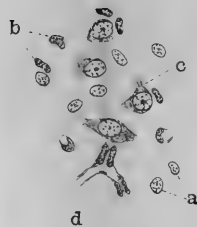


Fig. 3

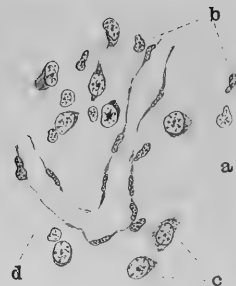


Fig. 5

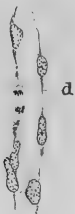


Fig. 4



Fig. 6

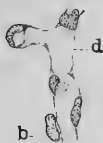


Fig. 7



Fig. 8

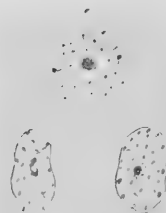
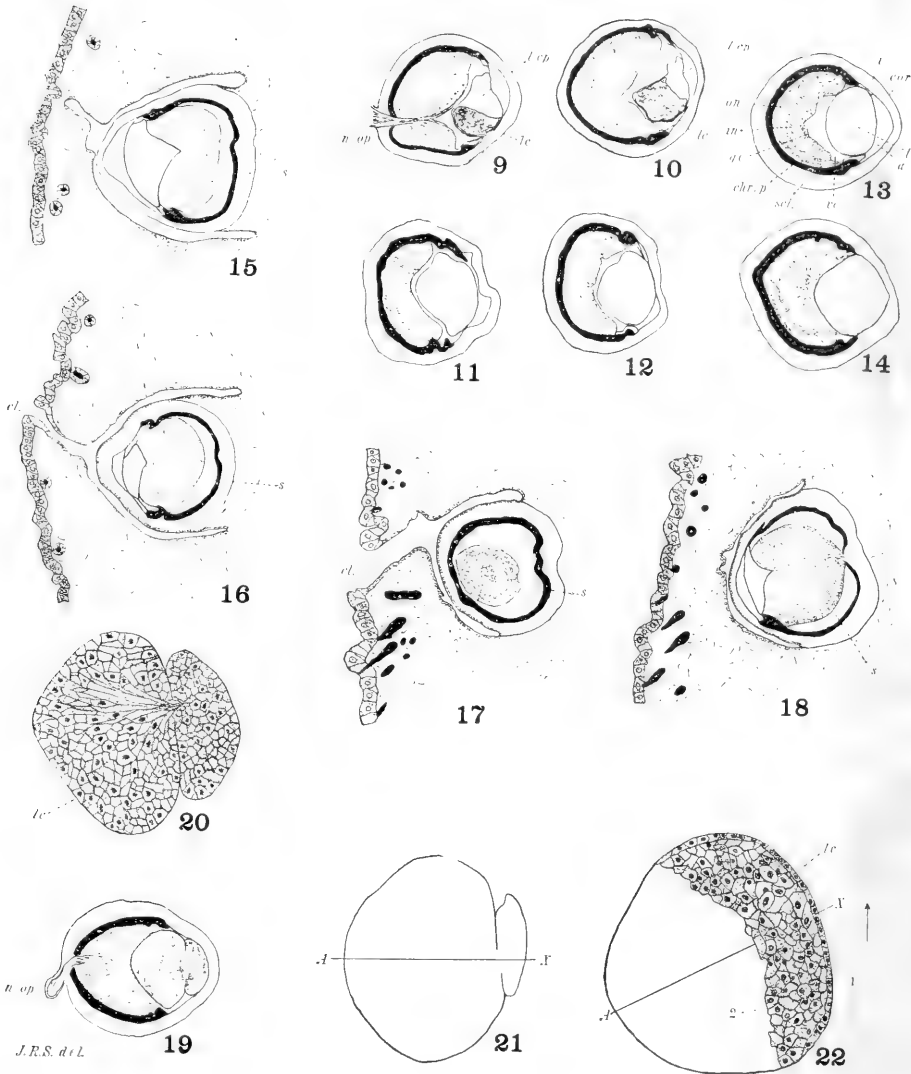
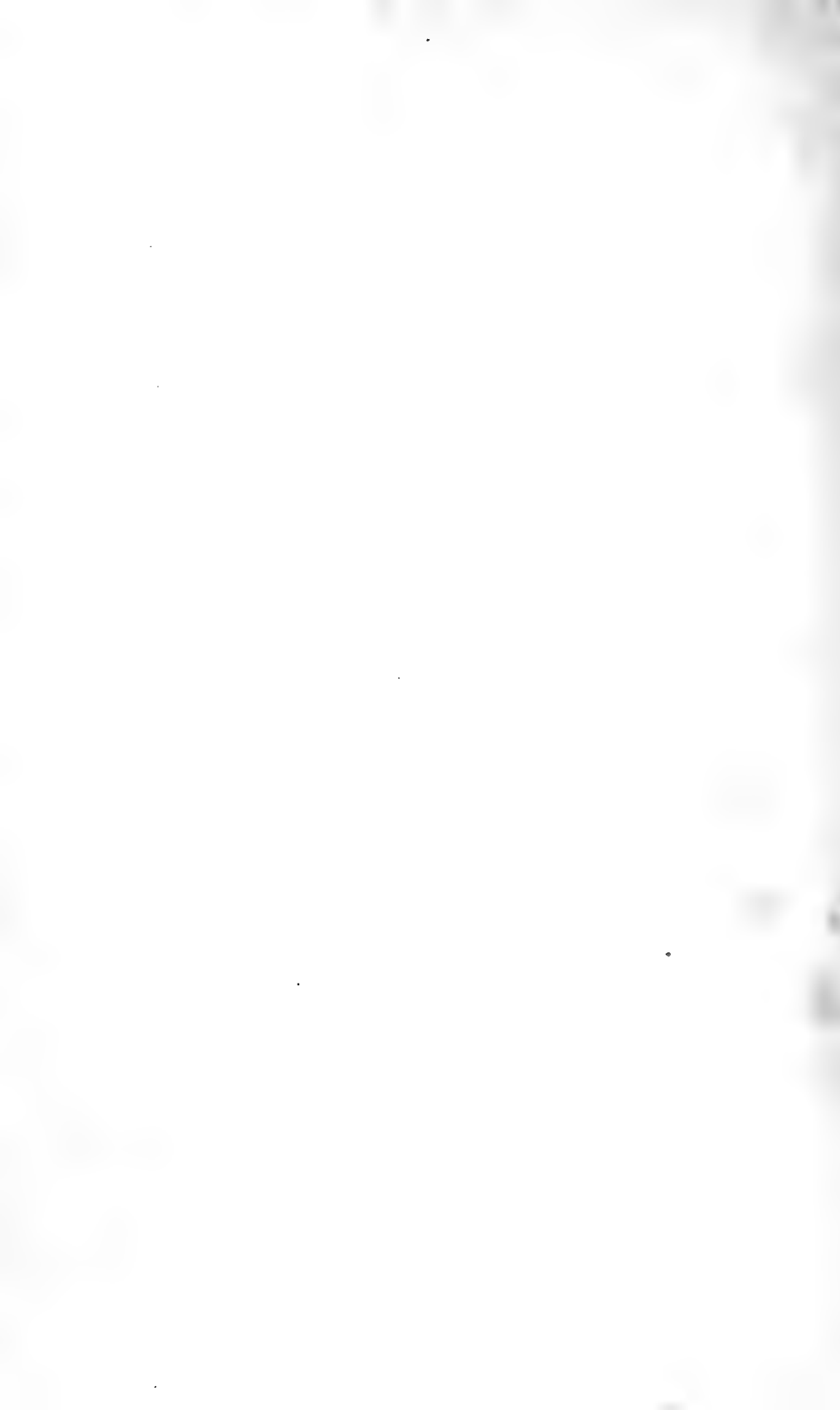


Fig. 9









RECENT LITERATURE.

Diseases of Orientation and Equilibrium.¹

The little volume of 291 pages is not a monograph in the sense of a collection of all the types of cardinal cases which are on record, but the publication of clinical lectures on a definite material of GRASSET'S own observation. This, in one way, implies some limitations of the discussion of the topic; on the other hand, it has the feature of freshness and directness so often found in French lectures.

The "documentary introduction" contains the records of 4 cases of tabes, 1 of diffuse myelitis, 3 of cerebral hemiplegia, 3 cases of cerebral lesion with autopsy, one case of organic lesion and hysteria, 1 of post-hemiplegic ataxia (with autopsy), 1 of praeparalytic hemichorea, 2 of cerebro-spinal syphilis, 1 of hysteria, 1 of lateral amyotrophic sclerosis, 1 of "chlorobrightisme," and one of cerebellar origin with autopsy. The second part discusses the anatomo-physiological data concerning the nervous apparatus of orientation and equilibration, the third the principal diseases in which it is involved, the fourth the symptomatology, with a study of the symptoms and the seat of the lesions, the fifth a synthetic summary and the 6th is devoted to principles of therapeutics.

The whole plan is highly to be commended. It is a move in the right direction: the writer starts from that which is open to observation and study in the living patient and groups around the needs of clinical explanation what data pathological anatomy and experiment can furnish, instead of starting from dead pseudo-anatomical wisdom to explain the symptoms, a plan which dulls the interest in clinical observation and leads to the notion that anatomy is the only salvation and aim of pathology.

In the anatomical part, G. recapitulates the facts under the heading of "centripetal paths of orientation," "centrifugal paths of equilibrium," and the "centres," in the concise schematic manner of the

¹ Les Maladies de l'Orientation et de l'équilibre. Par J. GRASSET. *Paris, Félix Alcan, 1901.*

clinical "anatomist." He opposes orientation (of the parts of the body among themselves, the body and the outside-world, and of objects among themselves) to equilibrium, a centripetal to a centrifugal feature of equilibration, which itself has its various superimposed centres.

To judge from the clinical evidence of BROWN-SÉQUARD paralysis and certain cerebral cases, the (afferent) paths of orientation are distinct from those of general sensibility in the spinal cord and in the cerebral cortex. G. distinguishes the apparatus of orientation of tactility, hearing and vision from that of kinaesthesia (general muscular sense, kinaesthetic path of the head (labyrinth), and kinaesthetic apparatus of the eyes), and points to the influence from the stomach in dizziness (pneumogastric). Anatomically he speaks of the column of CLARKE and the direct cerebellar tract, its termination in the opposite cerebellar cortex and the connection of the cerebellar hemisphere with the red nucleus and the parietal cortex of the opposite side—hence a double decussation.

The centrifugal path consists of 1, the pyramidal tract, 2, the descending cerebellar tract, and 3, the bundle of MONAKOW (faisceau rubro-spinal).

The centres of orientation and equilibrium are: 1. The cerebellum and its peduncles.

a. The inferior peduncle with the afferent elements from the trunk and, in the inner segment, the cerebello-vestibular apparatus plus the connection with the eye-muscles. The efferent elements from the nuclei of DEITERS and BECHTEREW form the descending cerebellar tract.

b. The middle peduncle gives a crossed connection with the hemisphere and also carries the optic impressions from the corpora quadrigemina and the nuclei of the pons (PAVLOW).

c. The superior cerebellar peduncle which unites the central nuclei of the cerebellum with the red nucleus. Through the latter impressions may pass directly to the perirolandic cortex and through the pyramidal tract to the anterior horns of the opposite side, or to the thalamus and then into the motor cortex and motor path.

2. The kinaesthetic area of the cerebrum.

3. The complex of elements of the anterior association center.

The cerebellar centres are grouped diagrammatically, similar to GRASSET's scheme of aphasia. He accepts a division into conscious orientation with voluntary equilibrium, and unconscious orientation with automatic equilibrium, and develops his reasons for the adoption

of a centre of conscious life in the frontal lobes and of a "polygone de l'équilibration" analogous to JACKSON's middle level.

The clinical and physiological discussions are very graphic and worth reading.

A. M.

Epilepsy, Hysteria and Idiocy.¹

As its predecessors, this volume gives an annual report on the service of Bicêtre and the Fondation Vallée, and the special classes for backward children. The second part contains a number of medical contributions, partly etiological, partly clinical, partly anatomical, none of which are of special importance from the point of view of comparative neurology, but of value to the worker on idiocy.

A. M.

Allis on the Cranial Nerves and Sense Organs of *Mustelus*.²

This important contribution to selachian morphology is based chiefly upon the study of three embryos in section, 36 mm., 55 mm., and 122 mm. in length respectively. It comprises 150 pages with three plates and shows the same conscientious attention to minute anatomical detail which characterizes ALLIS' previous papers, and much of morphological value is brought out.

In the discussion of the eye-muscle nerves the facts which have come to light since he published his *Amia* paper in 1897 are reviewed. I think that all students who have devoted any special attention to these intricate problems will agree with his concluding remark: "It is evident that it is useless to speculate on the subject until further facts have been accumulated."

On p. 178 he summarizes his evidence for pre-oral branchial arches as follows: There are thus two pre-oral arches indicated in embryos of *Mustelus*. In each arch there are what are considered by GEGENBAUR as remnants of the cartilages of the arch, and I now further find not only muscles definitely related to one of the arches, but also nerves that certainly might be considered as the pre- and post-trematic branches of each arch. The nervus trigeminus would then be a nerve formed by the fusion of at least three segmental nerves, and the ramus maxillaris superior trigemini would probably contain the pharyngeal elements

¹ Recherches Cliniques et Thérapeutiques sur l'Epilepsie, l'Hystérie et l'Idiotie. Par BOURNEVILLE. Paris, Progrès Médical, Vol. XXI, 1901.

² ALLIS, E. P. The Lateral Sensory Canals, the Eye-muscles and the Peripheral Distribution of Certain of the Cranial Nerves of *Mustelus laevis*. Quart. Jour. Micro. Sci., XLV, 2, 1901.

of all these nerves, in addition to containing, in its proximal portion, certain of their pre- and post-trematic elements."

The discussion of the chorda tympani is important, not because of the presentation of any additional facts tending to fix the homologies of this perplexing nerve; but rather by reason of the discovery of fresh difficulties in the way of current interpretations. Most recent writers, who accept the gustatory or communis character of the chorda tympani, hold that this nerve in the mammals is pre-spiracular, i. e., it lies morphologically cephalad to the Eustachean tube. ALLIS finds this open to question and reviews the facts among the fishes and amphibians in the light of the possibility of the post-spiracular position of the chorda. "The subject clearly needs further investigation, and first of all it is absolutely indispensable to know the definite relations of the chorda of mammals to the spiracular cleft."

But these matters are really of less morphological interest than the discussion of the homologies of the ampullary organs, which forms the point of departure and motive for the entire research. In his introductory paragraph he writes, "I have long had a very decided impression, opposed to that of most workers on the subject, that these ampullary organs must be genetically related to the terminal buds of ganoids and teleosts, rather than to the pit organs of those fishes." Mr. ALLIS admits at the start that he has wholly failed to find any positive evidence for this view, but adds, "Careful consideration of these observations has fully convinced me, though indirectly, that the ampullary organs do represent the terminal buds of ganoids and teleosts, and not the pit organs."

This conclusion has far-reaching applications, not apparent on the surface perhaps, to many of the major problems now at the fore in neurological morphology, viz. to all those problems connected with the systems of nerve components either in the periphery or in the centers and with the functional subdivision of the brain into neurone systems in general. It is therefore important that the indirect evidence upon which it is based be examined in some detail, since, as stated, it is "opposed to that of most workers on the subject."

The ampullae of LORENZINI of elasmobranchs, it will be recalled, are small sense organs lying at the bases of long unbranched tubes which open freely on the surface of the skin. The openings of these tubes are scattered widely and tolerably uniformly over the surface of the head, but the sense organs at the bottoms of the tubes are clustered in well defined groups and are innervated by nerves closely related to those of the adjacent lateral line canals. Previous authors generally

have assumed that these ampullary organs are differentiated parts of the lateral line system of sense organs, and many have compared them with the lines of pit organs of ganoids and teleosts. These pit lines are variously developed in different species of fishes, but are always arranged according to a tolerably definite and uniform pattern, and it would appear that they may in some cases be represented topographically by true lateral line canals and that in other cases the typical canals may be represented by similar rows of naked pit organs. These lines of pit organs therefore undoubtedly represent imperfectly developed lateral line canals.

Now, Mr. ALLIS calls attention to certain lines of organs (not ampullae) in the sharks which, together with some segments of the canal system of these fishes, appear to represent the characteristic lines of pit organs in ganoids and teleosts. He therefore concludes that the ampullary organs of elasmobranchs cannot represent the pit organs of higher fishes since these are otherwise provided for. This conclusion is reenforced by the important observation that in the younger embryos examined the ampullary organs arise scattered over the whole surface of the skin *at the positions of the pores of the ampullae*, not in the positions of the clustered sensory ends of these tubes in the adult. I quote a part of his description: "The ampullae in my 55 mm. embryo were nearly all represented by small teat-like processes that arose from the inner surface of the ectoderm, and projected into the underlying tissues. Some of these processes seemed solid, while others contained a small central lumen which sometimes led to the outer surface, the process then appearing as a sharp fold of the entire ectoderm. A small nerve was easily traced to the inner end of each process. While no attempt was made to trace the complete and definite distribution of these little processes, it was easily to be seen that in certain places they had exactly the relations to the lateral canals that the surface pores of the ampullary tubes have in the 12.2 cm. embryo. This seemed to me to indicate that it must be the pore in the adult, and not the ampulla, that indicates the place of origin of the structure. Here, then, from the primary distribution of these organs, as indicated by their surface pores, was perhaps a manner of determining whether they arose from pit organs or from terminal buds. . . . The long ampullary tube that is found in the latter embryo must then be formed by an exceedingly rapid growth of the short process of the younger one, that process being, so to speak, stretched out into a long tube between the fixed point represented by its surface opening and another relatively fixed one, represented by the point where the sensory nerve enters the

process. The tube apparently offers less resistance to this stretching process than the nerve does."

ALLIS therefore concludes (1) that the ampullary organs do not correspond to the pit lines of higher fishes, a conclusion that is doubtless correct; and (2) that the ampullary organs do correspond to the terminal buds of the higher fishes, a conclusion by no means following from the premises, as I hope to show immediately.

Now, in the case of *Ameiurus* I have shown, in a paper published in this Journal since Mr. ALLIS' work went to press, the presence of lateral line canals and pit lines conforming to the usual teleostean pattern, and in addition two sets of sense organs distributed freely in the skin according to no definite pattern so far as determined. One of these comprises the terminal buds, which are strictly typical in structure and innervation; the other, a type of small sense organs structurally resembling the neuromasts or organs of the lateral line canal system and unmistakably innervated by lateralis nerves, terminating in the tuberculum acusticum like those for canal organs and organs of the pit lines. The latter organs I termed "large pit organs" to distinguish them from the much more numerous "small pit organs" freely scattered in the skin as mentioned above. These small pit organs, which seem not to be present in teleosts generally, may perhaps be directly compared with the embryonic ampullary organs of the sharks, but the terminal buds, never. The argument from the arrangement of the pores of the ampullae therefore falls to the ground.

Again, the terminal buds of ganoids and teleosts are known to be innervated by visceral sensory or communis nerves, while there is strong presumptive evidence (not amounting as yet to demonstration) that the ampullary organs are innervated by lateral line nerves, a system which has absolutely no morphological connection with the communis nerves. ALLIS meets this by attempting to show that the innervation of the ampullae of selachians is not necessarily the same as that of the lateral line organs and that it may be homologous with that of the terminal buds of higher fishes. The argument here is involved and rather difficult to follow, but as I understand it, it rests on the assumption (a pure assumption with no basis of observed fact) that the ampullary organs are innervated exclusively from the so-called lobus trigemini and that this lobe of elasmobranchs is homologous with that of some teleosts, and of *Acipenser*. These assumptions were suggested by STRONG in 1895, but the latter one has been given up by morphologists generally, including Dr. STRONG himself, if I mistake not, as untenable. This second assumption grows out of a most unfortunate con-

fusion of terminology which has, however, been completely cleared up by the combined efforts of several very recent authors. Briefly, the "lobus trigemini" of Acipenser is now definitely known to be exclusively a lateralis center and should be termed the lobus lineae lateralis (JOHNSTON). It has nothing to do with the innervation of terminal buds. The same is almost certainly the case regarding the so-called lobus trigemini of elasmobranchs, as JOHNSTON has pointed out in the last issue of this Journal (p. 61). It doubtless does innervate some (but not necessarily all) of the ampullary organs, these being modified lateralis organs. The so-called lobus trigemini of teleosts (e. g., Ameiurus), however, is certainly a center for fibers from terminal buds of the outer skin and should be termed the lobus facialis. KINGSBURY suggested these homologies in this Journal in 1897 and all subsequent research has confirmed them. That ALLIS has perpetuated the confusion of these structures at so late a day as this is striking illustration of the value of the suggestion of a recent writer that the term lobus trigemini should be finally dropped from our nomenclature at once. When once these relations are clearly recognized, the whole morphology of the cutaneous sense organs of the fishes, and of their centers in the brain as well, becomes for the first time intelligible and it is greatly to be regretted that the confusion of the past century should be carried over into the new, as Mr. ALLIS seems to have done in this paper. This is the more surprising since it is to him that we owe one of our most convincing proofs of the morphological distinctness of the lateral line system as a whole.

C. J. H.

Edinger on the Selachian Cerebellum.¹

Professor EDINGER's late contribution upon the selachian cerebellum contains points of special interest. Under "*Form und Schichtung*" the author describes briefly the general form of the cerebellum and its layers, and the nucleus lateralis cerebelli. This nucleus is situated in the midst of the most caudal fibers of the "Kleinhirnschenkel" and may represent Deiter's nucleus of higher vertebrates. More special attention is given to the "*Faserung*." The fiber tracts are treated in three categories, "Eigenfasern," "Verbindungen des Kleinhirnes mit anderen Hirntheilen," "Fasern aus den sensiblen Hirnnerven." The "Eigensystem" is very pronounced. Besides fibers uniting parts of

¹ L. EDINGER. Das Cerebellum von Scyllium canicula. *Archiv für Mikroskopische Anatomie und Entwicklungsgeschichte*, 58 Bd. 4 Heft, pp. 661-677, Taf. XXXIII und XXXIV.

the same side of the cerebellum, the greater part of the decussatio cerebelli belongs to this system. The tractus cerebello-thalamicus cruciatus, the most mesial of the second category, forms into two bundles in the base of the Mittelhirn and, decussating in the region of the oculomotorius, ends in the gray matter dorsal and lateral of the infundibulum. The tractus cerebello-mesencephalicus passes obliquely to its apparent termination anterior and lateral of the ganglion interpedunculare. Immediately upon the termination of these fibers, however, there appears a new bundle which without doubt ends in the nucleus pretectalis. The tractus cerebello-spinalis passes into the cerebellum by an anterior part and a much stronger posterior part. The latter passes directly over the nucleus cerebelli, from which it appears to receive fibers, from the lateral periphery of the medulla. The anterior part of this tract cannot be so certainly followed and may not belong to this system. The fibers of the tractus cerebello-tectalis collect themselves out of the deepest fibers of the Mittelhirn roof and may arise from cells of the nucleus magnocellularis which is usually assigned to the trigeminus. The entire tract disappears in the velum anticum caudal of the decussation of the trochlearis and may possibly be a dorsal trochlearis root and not a cerebellar tract. The tractus cerebello-spinalis ventralis is probably represented by the more lateral and larger of the tracts from the decussatio veli, which is dorsal and anterior of the decussation of the trochlearis. This tract passes caudad and ventrad peripherally of the ganglion isthmi into the medulla. From the vagus, glossopharyngeus, acusticus and trigeminus fibers pass directly into the cerebellum. B. HALLER's "obere äussere Wurzel des V." is assigned to the ramus lateralis facialis. This root may not send fibers into the cerebellum proper but its terminal nucleus, in the lobus acustico-facialis, is covered by the true cerebellar cortex so that the essential cerebellar connection probably exists. The author concludes: "dass das Kleinhirn der Selachier im Wesentlichen nur Endstätte der directen sensorischen Bahn aus den Hirnnerven ist und dass alle anderen in es eingehenden Fasern nur eine kleine raumliche Rolle spielen."

In tracing nerve fibers into the cerebellum Professor EDINGER has employed successfully the degeneration methods of MARCHI and ALGHIERI. He found difficulty, however, both in securing proper degeneration of the tracts, partly on account of the early death of the specimens, and also in interpreting the degeneration results, since regions clearly out of connection with the affected centers showed degeneration phenomena. The latter may in some cases be due to the more active metabolism.

G. E. COGHILL.

Pershing's Diagnosis of Nervous and Mental Diseases.¹

"The object of this book is to facilitate the recognition of nervous and mental diseases by physicians who are not specialists in neurology."

It is arranged after the method of a botanical key. After a general introduction with details about the method of examining various features (page 17-65), the author gives short chapters on "the recognition of organic diseases, the principles of localization, the signs of hysteria, the diagnosis of neurasthenia, and mixed forms of diseases" (page 69-86). The key for the special diseases covers pages 86-217.

Where we deal with more definite entities, as species and genera of zoology, or elements with definite compounds in chemistry, and fairly definite units, as in mineralogy, the method undoubtedly has more justification than in this special field where with the decision upon the name frequently we are quite far yet from an appreciation of the whole condition, which after all should be implied in a diagnosis. While a number of the tables for differential diagnosis given in the book are very useful, the book cannot try to make unnecessary the available text-books of nervous and mental diseases, and as a supplement of these books it is rather expensive and by no means easy to use for one not familiar with the larger works.

In many portions, especially that on insanity, it must offer very little relief to the physician to have found such names as mania, melancholia, stuporous insanity, and a whole string of insanities named after their cause, as puerperal, lactational, phthisical, carcinomatus, myxoedematous, hysterical, etc. But these are faults of the present status of these branches of medicine which, however, are seriously in the way of the key-method.

It would probably be of great advantage for the book and the reader if the "key" applied to some definite standard work and practically were a part thereof.

A. M.

¹ The Diagnosis of Nervous and Mental Diseases. By HOWELL T. PERSHING, M.Sc., M.D. Professor of Nervous and Mental Diseases in the University of Denver; Neurologist to St. Luke's Hospital; Consultant in Nervous and Mental Diseases to the Arapahoe County Hospital; Member of the American Neurological Association. Illustrated. 12mo. Published by P. Blakiston's Son & Co., 1012 Walnut St., Philadelphia. 1901. Price, in cloth, \$1.25 net.

Koelliker on the Brains of Monotremes.¹

Under this title Professor KÖLLIKER treats the indicated portion of the brains of *Ornithorhynchus* and *Echidna* separately, about two thirds of the space being given to the former. In both cases the method of treatment is the same: a description of a series of transverse sections (18 of *Ornithorhynchus* and 9 of *Echidna*) followed by a descriptive and comparative study of the particular parts as they appear throughout the section-series. In his resume of results the author calls attention to the following important features: The fourth ventricle is proportionately much longer than in other mammals. The pyramidal decussation is very feebly developed and the pyramidal tracts, indistinguishable anteriorly, are at best ill defined in the posterior parts of the medulla. The more distal course of the fibers is either in the "Seitenstrang" or in BURDACH'S column. There is a typical fillet which is stronger in *Echidna* than in *Ornithorhynchus*, while the nucleus gracilis in both animals is small as compared with the nucleus of BURDACH'S column. The "nucleus lateralis" (n. of lateral tract in the medulla) is much better developed in *Echidna* than in *Ornithorhynchus*. The nucleus of the hypoglossus, as compared with that of other mammals, is located much more laterally, and the root fibers pass "medio-ventralwärts" to their exit. The accessorius is much stronger in *Echidna* than in *Ornithorhynchus*. Its root fibers penetrate the tuberculum quinti in *Echidna* while in *Ornithorhynchus* they pass first between the "fasciculus lateralis" and the tuberculum quinti and then penetrate the latter. The nucleus ambiguus and the end nucleus of the fasciculus solitarius are very strongly developed in *Echidna*. The nervus cochlearis enters the medulla with the nervus vestibularis ventrally of the posterior cerebellar peduncle. The acoustic nerve is very large in *Echidna* and very small in *Ornithorhynchus*. There occur in both animals two distinct facial motor nuclei, a dorsal and a ventral, while the former in *Echidna* shows a tendency to separate into four groups of cells. The facial nerve is small in *Ornithorhynchus* and large in *Echidna*. A longitudinal spino-cerebral tract, the "Zonalbahn," associated posteriorly with the quintus descendens, joins the "Bindearm" in *Echidna* but is absent in *Ornithorhynchus*. The oculomotor nucleus in a single group of cells without crossed fibers. The inter-olivary lemniscus medialis is composed of fibers from the fillet, secondary trigeminal fibers, and

¹ A. KÖLLIKER. Die Medulla Oblongata und die Vierhügelgegend von *Ornithorhynchus* und *Echidna*. "mit 27 zum Thiel farbigen Abbildungen im Text," 100 pp. quarto. Leipzig, 1901. Wilhelm Engelmann, 16 M.

“Brückenfasern.” A longitudinal tract of uncertain origin out of the medulla, the “ZIEHEN’schen Bündel,” joins the “Bindearm.” The nervus cochlearis, the superior olive and the “Trapezfasern” are exceedingly reduced in *Ornithorhynchus* while they are well developed in *Echidna*. The corpus quadrigeminum distale and the nucleus lemniscus lateralis, also, are larger in *Echidna* than in *Ornithorhynchus*. In the pons of *Echidna*, and especially in *Ornithorhynchus*, are “dorso-ventral” fibers appearing to rise partly from the fasciculus longitudinalis dorsalis and partly from the nucleus of the pons. A “fasciculus longitudinalis medialis” connects the ganglion interpedunculare with the ganglion tegmenti dorsale.

This monograph is presented in beautiful form and is precise and thorough in treatment. It is a valuable contribution to the morphology of the monotreme brain.

G. E. COGHILL.

Polish Archives for biological and medical Sciences.

This new periodical contains translations in French or German of scientific memoirs in the Polish language which appear simultaneously either in the Polish edition of the Archives or in other Polish publications. It also contains a bibliography as complete as possible of all works or articles on biological and medical subjects appearing in the Polish language, together with both French and German translations of their titles. The first number of the French and German edition contains 252 pages with several plates and is very commendable both in matter and form. The Archives are edited by Professor H. KADYI and a large staff of collaborators; published at Lemberg at M. 40 (50 francs) per volume.

Micro-chemistry of Nerve Cells.¹

A careful study of the micro-chemistry of nerve cells leads the author to the conclusion that there are at least three distinct nuclein compounds in nerve cells, the NISSL granules, the basophile substance covering the nucleolus and the oxyphile substance of the nucleus. Each of these bodies contains iron and phosphorus, the usual constituents of many nucleo-proteids. The three compounds above mentioned are genetically related, a study of developmental stages showing that they are derived from the chromatin of the nucleus of the germi-

¹ SCOTT, F. H. On the Structure, Micro-chemistry and Development of Nerve Cells, with special Reference to their Nuclein Compounds. *Trans. Canadian Institute*, VI, 1898-99.

nating cell. This chromatin divides into two parts, each containing iron and phosphorus, but the one is oxyphile and remains in the nucleus, while the other is basophile and diffuses into the cell body and becomes the Nissl granules. A portion of the nuclear chromatin, however, remains unmodified about the nucleolus. The Nissl granules are regarded as morphological elements, composed of one substance which has the same refractive index during life as the cytoplasm.

C. J. H.

Histogenesis of Peripheral Nervous System in Teleosts.¹

This careful research contributes welcome data on one of the vexed questions of the day. The development of the salmon is traced step by step until the peripheral nervous system is fully laid down. The exposition is characterized by unusual clearness of statement and the figures in particular are very convincing. The author supports throughout the doctrine of His that every nerve fiber arises from a single cell, as opposed to the cell-chain theory. He finds, it is true, cells migrating out from the spinal cord with the ventral root fibers, such as are described by the advocates of the latter theory. These cells, however, follow the outgrowth of the axis cylinders of the ventral roots and Dr. HARRISON'S interpretation of them is different from that of any of the other recent students of this problem. In fact, he thinks it probable that they enter into the formation of motor sympathetic ganglia.

The neural crest is carefully described and its peculiar development in the teleosts put into relation with its simpler history in other vertebrates. The history and significance of the giant cells, or *Hinterzelle*, are treated very fully. They arise in that portion of the medullary cord which corresponds to the neural crest and differentiate into two forms. The first sends out a T-process, one limb of which ascends, the other descends in the dorsal column. The second form is similar, but sends out in addition to the other processes a peripheral process which enters the dorsal root and terminates as a sensory fiber in the skin. This peripheral distribution is a primitive one, and these cells are homologous with spinal ganglion cells, also with the middle-sized (not the colossal) bipolar ganglion cells of *Amphioxus*, with the dorsal cells of *Petromyzon* and with the transitory nerve cells of *Elasmobranchs*. They are sensory elements which fail to wander out into the

¹ HARRISON, ROSS GRANVILLE. Ueber die Histogenese des peripheren Nervensystems bei *Salmo salar*. *Archiv f. mikr. Anat.*, LVII, 1901.

peripheral position of the spinal ganglia, and in salmon embryos they are for a long time the only sensory elements provided with peripheral nerves. They differentiate simultaneously with the motor nerves and commissural cells and disappear when the spinal ganglion cells are ready to function.

C. J. H.

Natural Subdivision of the Cerebral Hemisphere.¹

Professor ELLIOT SMITH's contribution on the Natural Subdivision of the Cerebral Hemisphere is based upon extensive studies in comparative anatomy and yields several points of great importance to the proper understanding of this part of the brain. They will be especially helpful in clearing away the existing obscurity because they are accompanied by exhaustive historical notes in which the various conflicting usages are clearly contrasted.

Nine distinct histological formations are recognized in the typical mammalian hemisphere, as follows :

- (1) The olfactory bulb.
- (2) The olfactory peduncle.
- (3) The olfactory tubercle (*tuberculum olfactorium*), a peculiar cortex which forms a cap upon the ventral aspect of the head of the corpus striatum.
- (4) The pyriform lobe. Its anterior portion is closely applied and attached to the lateral aspect of the striatum and extends forward so as to pass into direct continuity with the olfactory peduncle. In its caudal part the pyriform lobe becomes free from the corpus striatum, and becomes a real "mantle" which extends in the caudo-mesial direction to become continuous with the hippocampus.
- (5) The paraterminal body, a large ganglionic mass, directly continuous in front with the olfactory peduncle, extending backward to the lamina terminalis and upward to fill the gap between the callosum and the psalterium.
- (6) The anterior perforated space.
- (7) The hippocampal formation, sharply differentiated into (a) the hippocampus (*sensu stricto*), and (b) the fascia dentata.
- (8) The corpus striatum.
- (9) The rest of the hemisphere, consisting of a dorsal cap, which is the "neopallium."

The grounds for the separation of the hippocampus and the "neopallium" are discussed at some length. "Hitherto the strange irony of

¹ SMITH, G. ELLIOT. Notes upon the Natural Subdivision of the Cerebral Hemisphere. *Jour. Anat. and Physiol.*, XXXV, 4, July, 1901.

a confused morphology has denied a name out of the plethora of cerebral nomenclature to be the exclusive property of this the dominant organ of the nervous system and the master-structure of the whole body; for it has been linked with the hippocampus, which does not share these high attributes, but has long since reached the height of its importance, and is now on the wane in those mammals in which the neopallium reaches its supreme development. A distinctive name—corpus callosum—is now very generally admitted for the commissural fibers of this neopallium, in contradistinction to those of the hippocampus—psalterium. Why, then, should not a like distinction be conferred on the cortical areas from which the commissures ultimately spring? . . . It must be obvious from the preceding discussion that the terms 'rhinencephalon' and 'pallium' cannot be employed as compliments the one to the other without considerable distortion of the original meaning of one or both of the terms.

"The pallium, in the strict sense, is composed of three distinct structural elements: a ventral part, or pyriform lobe, the '*basipallium*,' the marginal pallium or hippocampus, and lastly that large dorsal cap, the '*dorsipallium*' or *neopallium*. If now we regard this term 'neopallium' as the compliment of 'rhinencephalon,' it will involve a new definition of the latter which would then include the whole pyriform lobe, the whole hippocampal formation and paraterminal body, in addition to the olfactory bulb, peduncle, and tubercle, and the locus perforatus. Far from such an employment of the term proving awkward, it expresses the obvious relationship of both the hippocampus and the pyriform lobe to the olfactory apparatus in so natural a manner as to afford the last convincing link in the chain of evidence for this rational basis of division into neopallium and rhinencephalon. . . . So far as I understand the question at issue, there are two, and only two, alternative meanings logically open to us for adoption. It [rhinencephalon] may be employed to designate the olfactory bulb and peduncle as OWEN used it, and as such is unnecessary, and therefore superfluous; or it may be used to include all those regions which are preeminently olfactory in function, and have become definitely specialized in structure in consequence. Such a definition will include the olfactory bulb, its peduncle, the tuberculum olfactorium and locus perforatus, the pyriform lobe, the paraterminal body, and the whole hippocampal formation."

C. J. H.

Jahresbericht f. Neurologie und Psychiatrie.¹

This is the fourth issue of this indispensable serial, containing the literature for the year 1900. The volume comprises 1135 pages of closely printed matter and some 6000 titles are given in the literature lists, a large proportion of which are accompanied by brief abstracts. The general plan of the work is as in previous issues, and is carried out with the same thoroughness.

The Flat Fishes.²

This memoir, in connection with a general account of the anatomy of Pleuronectes, gives a discussion of the nervous system which is of importance to comparative neurologists. The description of the brain is brief and confined mainly to externals. The peripheral nerves and sense organs are, however, very fully and critically treated. The peripheral nerves are described from the point of view of the doctrine of nerve components and the 50 pages devoted to them would form one of the best introductions to this doctrine available. The nerves were reconstructed from serial sections and thus the exact composition of each can be stated from direct microscopic study. In this way another type is added to the rapidly growing list of vertebrates whose peripheral nerve components are accurately known.

Pleuronectes conforms to the teleostean scheme as already exemplified by Gadus, Menidia and Ameiurus with remarkable fidelity. It is interesting to note that it also possesses a vestigial nervus ophthalmicus profundus, whose relations are almost exactly the same as those described by the reviewer in 1899 for Menidia. Thus there are three types (including Trigla of STANNIUS' descriptions) among the teleosts now known to possess a vestige of this nerve.

Of still more general biological importance is the discussion of the asymmetry of the flat fishes. The authors first dispose of the idea that the left eye passes through the substance of the head to the right side and also of "the mischievous assumption that the left eye has travelled over the top of the head to the right side. The *fact* is that the left eye is *not on the right side at all*. Its presence there is purely illusory. What

¹ Jahresbericht über die Leistungen und Fortschritte auf dem Gebiete der Neurologie und Psychiatrie. Edited by Prof. E. MENDEL and Dr. L. JACOBSON, with the cooperation of Dr. E. FLATAU and a board of 58 collaborators. Berlin, S. Karger, 1901.

² COLE, F. J and JOHNSTONE, JAMES. Pleuronectes (The Plaice). Liverpool Marine Biology Committee Memoirs, No. 8. 260 pp., 11 plates. London, Williams & Norgate, Dec., 1901. Price 7 s.

has happened is that the *whole* of the cranium *in the region of the orbit* has rotated on its longitudinal axis to the right side, until the two eyes, instead of occupying a horizontal plane, have assumed a vertical one, and the left eye is *dorsal* to the right. *Then* the dorsal fin grew forwards over the roof of the cranium, but naturally cannot define the morphological right and left sides of the orbital region. Thus the ocular side comprises not only the right side but a portion of the left, and the true morphological median line lies *between* the two eyes and not *above* them. The relation of the eyes to the skull is, notwithstanding the rotation of the orbital region of the latter, exactly the same as in a symmetrical fish, and the only differences of importance are the atrophy of the anterior portion of the left frontal, and the purely secondary junction under the left eye of the left prefrontal and frontal."

C. J. H.

RECENT LITERATURE.

The Mental Factor in Medicine.¹

"Some bold quack by mere force of assertion will give her the will to bear, or forget, or suppress all the turbulences of her nervous system." Thus writes Sir JAMES PAGET of a clever, charming, widely known lady and says: "What unsatisfactory cases these are!" SCHOFIELD undertakes to reclaim some of the successful and therefore legitimate methods of the quack for the medical man and gives a rather entertaining review of views of others, and many bright observations of his own to show the absurdity and the harmfulness in the medical man who leaves out mind in his "scientific" consideration of the patient.

In principle, Dr. SCHOFIELD deserves credit for his effort. And since he makes the book quite readable by a current epitome on the margin and a brief summary at the end, we can heartily recommend it to a glance of even hurried readers, as a book which expresses a widely held standpoint in the efforts to cure the materialistic one-sidedness of medicine.

This stand-point is the assumption of unconscious mind as compared to which the conscious mind is very limited and of little influence on the body. His exposé shows many of the snares and fallacies of this view so well that it is a great temptation to enter upon it critically.

The author would strengthen the persuasive quality of his book by not introducing the unconscious mind as long as it is really a bug-bear to many thinkers, also among physicians. He can give all the strong facts of his argument without this ballast, but he has probably done well in giving it to us because its lack of convincing necessity is more easily seen in his simple statement than in the armored constructions of philosophers of profound dialectic training.

Chapter II. attempts to prove that as the action of the mental factor in disease is unconscious, it cannot be recognized as mental by those who limit mind to consciousness. The word "mind" must therefore be extended to include all psychic action.

¹ The Force of Mind, or the Mental Factor in Medicine. By ALFRED T. SCHOFIELD, M. D., M. R. C. S., &c. Philadelphia, P. Blakiston's Son & Co., 1902. Price \$2.

"This, I trust, is evident to all who have followed the line of argument. The mind is one and indivisible. Part of it is seen by the mental faculty or eye we call consciousness, just as part of our body is open to our gaze. The rest is no less mind because beyond the range of vision, any more than those parts of the body are not corporeal which are outside the range of sight. Their existence can be easily proved by other faculties, just as the unconscious mind can be proved without the aid of consciousness. I say nothing of double consciousness, as I cannot here speak of consciousness as being any other than that with which we are familiar in our normal state. There may be other consciousnesses; for our purpose they are termed 'unconscious.'

"The narrow range of the conscious mind, compared with the wide field of the unconscious, has been also noted here."

This epitome is sufficient to show a common fallacy which I try to exemplify as follows:

Any experience (I use this word in preference to the too specialized words sensation, emotion, because nothing is purely sensation, or emotion, etc.), whether it appears prominent at the time of its occurrence or not, implies a certain attitude of the person which, like all attitudes, is apt to recur. We know of biological organisms that what is commonly called memory is fundamentally the likelihood of recurrence of attitudes, with more or less definition. We know also that an attitude may persist without our paying conscious attention to it. The existence of likelihood of recurrence, the possibility of using the partial recurrence, is what we call memory, and it is not necessary to assume with HERBART that a sort of permanent jumping-jack arrangement of permanent ideas exists which is difficult to imagine psychically, and impossible even with the ideas of "deposits" and vestiges" in the morphological field. What is undeniable and sufficient is the existence of a greater readiness for attitudes once actually experienced—a thing totally different from an actual 'mind,' in the sense of mental activity, but evidently what is commonly implied by the term "unconscious mind."

Let us replace SCHOFIELD's simile of the persistence of the parts of the body which are not in sight, by one more in point for a functional phenomenon.

The work of a cobbler gives his hand a very definite shape which makes it adapted to the work, and allows an experienced observer to recognize promptly the occupation of the person. Yet, the adaptation, the morphological attitude, would never be confused with the occupation itself, as a permanency of actual occupation, but merely as evi-

dence for the past and for forecasts for the emergency of a renewed trial of the occupation—we should expect that such a hand has done the work and will very likely be adapted to doing it probably again. In the case of mental activity, we may say of a hysterical patient: she has at one time gone through an experience which gave her a fixed idea. The attitude has never been corrected; everything that goes on is done with the attitude as an actual factor, although the “fixed idea” as such can be revived only under specific circumstances, and although the attitude does not express itself in the conscious life of the patient, except perhaps in hypnoid conditions. Or, to take the instance given by SCHOFIELD of a young man scared into hypochondriasis by his physician. The attitude impressed on the patient is not favorable for a cure; part of it manifests itself when he thinks and argues and even if he seems distracted, the attitude lingers “unconsciously.” “Faintly conscious” is not unconscious; and what is really unconscious is merely persisting as an attitude.

In the cobbler nobody would call the shape of the hand “unconscious occupation”; in the “mental” attitude of the patient it would perhaps also be better to avoid the term “unconscious mind,” and to stick to the indisputable fact of the unfavorable attitude which shows itself “actually,” though not necessarily “mentally,” in the form of a very definite psychic process.

The criticism is therefore not one of SCHOFIELD’S facts, but one of an encumbrance by unessential dogmata such as “the mind is one and indivisible.” These will act like a bugaboo with many who would do well to take in all the facts presented in the book, and will induce them to put the book aside.

Perhaps my position will be fitly expressed by a transcription of the summary of Chapter III., which is intended to prove the thesis that “the double action of the mental factor on the body in health consists *generally* in carrying on the functions of life, and *pecially* in physically expressing mental states.” I should say: it consists *generally* in carrying on *some* functions of life (in order not to force upon the reader an unessential and possibly objectionable exclusively idealistic conception of life), and *pecially* in making those physical states possible which, without mental states, would be inconceivable, or at least which are not known to occur empirically without mental states, *or without their help*. The latter is possible also through mere attitudes once produced mentally, i. e., the “unconscious” of SCHOFIELD.

With some such transcription of what is meant by the, for many, mystifying terms “unconscious mind,” the author’s argument would

gain in clearness. For instance his Chapter XI. shows that "the affective agent in all faith cures is the unconscious mind." For this we should say: The affective agent in all faith cures is the getting at, and correcting of, mental attitudes, and also merely mentally *induced* attitudes of the person which are incompatible with health.

There are probably better presentations of the same topic. But since they are usually not as entertaining, the plea of Dr. SCHOFIELD is not to be disregarded, and with certain readers it will have a good effect. We repeat, however, that a modest pluralistic attitude would be a better ground than the dualistic assumption which is probably more useful for certain schools of moralists than for the physician.

ADOLF MEYER.

Chase's General Paresis.¹

"General Paresis" by ROBERT HOWLAND CHASE, A. M., M. D., physician-in-chief of the Friends Asylum for the Insane of Philadelphia, is more in the nature of a popular exposition, especially of the clinical aspects of this disease, and is adapted to the purposes of the general practitioner rather than to those of the alienist. The first portion of the book deals with the various stages of the disease, which are divided into prodromal and first, second and third stages of the established disease. This is followed by two chapters devoted to varieties of the disease, including galloping, circular, melancholic, spinal, juvenile, senile, simple progressive dementia, and paresis in women. The next five chapters are devoted to symptomatology of the various types of the disease in the different stages, followed by one chapter each in differential diagnosis, etiology, pathology and treatment. The chief etiological factors mentioned are heredity, alcoholism, excessive venery, mental overstrain, excitement and syphilis, no new phases of this question being brought out. The discussion of the pathology of the disease is largely a review of the findings of MICKLE, W. FORD ROBERTSON, BEVAN LEWIS and BERKLEY. BEVAN LEWIS and BERKLEY advocate the view that the blood vessels are the primary seat of the lesion; W. FORD ROBERTSON that the disease depends upon the occurrence of a general toxic condition, the exact nature of which is still obscure but which is certainly in many cases the result of antecedent syphilitic infection causing first changes in the blood vessels followed by degeneration of the cortical neurones; finally NISSEL, TUCZEK, F. W. MOTT and others advocate the view that the neurone is affected primarily. Nothing new in treatment is suggested. Although

¹Published by P. Blakiston's Son & Co., Philadelphia. 1902.

the author states that his experience in mental diseases covers a period of more than twenty-five years with extensive observations upon every phase of this disease, yet all his illustrative cases are quoted from the writings of various alienists, especially those of CLOUSTON, BEVAN LEWIS, STEARNS, SANKEY, FOLSOM, HAMMOND, SPITZKA, SAVAGE, CAMPBELL CLARK, BERKLEY, DERCUM and E. D. FISHER. On the whole the book, of nearly 300 pages, is well written and includes all the salient features of the subject without treating any of them exhaustively.

G. ALFRED LAWRENCE, M. D., PH. D.

Researches in Psychopathology.¹

This well printed volume contains six studies in psychopathology conducted in the psychopathologic hospital under the direction of Dr. SIDIS. These studies are preceded by a section of 32 pages by the Director entitled, "Some General Remarks Concerning Psychopathological Research," written in a literary style too discursive and prolix to be easy reading. The cases which are presented in the succeeding studies are, however, of great interest. The underlying motives of these studies can best be presented in the words of Dr. SIDIS' summary as given in the Introduction to the volume, from which the following extracts are taken:

"The present researches form a series of cases, the investigation of which is undertaken with the object of studying the problems presented by the phenomena of functional psychosis. Out of a mass of material we have selected a few cases typical of many others, each case standing for a type. As much as possible we have tried to avoid theories and principles and give simply a résumé of the facts and experiments."

"The first study of the series presents an investigation of the main phenomena observed in dissociative states of functional psychosis. An account is given of some of the methods of bringing about a synthesis of subconscious dissociated systems. The study specially relates to psycho-motor reactions of subconscious systems. Different methods are worked out to obtain subconscious reactions to stimulations. The extent and intelligence of the dissociated subconscious systems are tapped in various ways. The results clearly reveal the nature of the phenomena of functional psychosis. Psychologically, *functional psychosis is coextensive with the whole domain of the subconscious*. Physiologically, *functional psychosis is correlated not with organic neuron degeneration, but with functional disaggregation of whole systems of neuron-aggregates*. In functional psychosis, the function apparently lost and de-

¹Psychopathological Researches. Studies in Mental Dissociation. By BORIS SIDIS and others. Published under the auspices of the Trustees of the Psychopathic Hospital, Department of the New York Infirmary for Women and Children. New York, G. E. Stechert. 1902.

stroyed is found to be present in the subconscious—the loss of function is purely dissociative. The activity is preserved and the system is really unaffected—it is only dissociated from other functioning systems.” “With the further progress of the pathological process the neuron itself becomes affected. In the early stages of the process of neuron degeneration, the function of the neuron is interfered with, though restitution is still possible. These stages include the vast domain of *functional* neuropathic disturbances, such as paralysis agitans, choreas, idiopathic epilepsy, and the neuropathic insanities, such as the various neuropathic forms of manias and melancholias, of periodical and circular insanities, of dementia praecox, of paranoias, and so on. Finally in the last stages of the process of degeneration, the neuron is destroyed and restitution is no longer possible. Tabes, general paresis, syringomyelia, the chronic insanities, amyotrophic lateral sclerosis, acute ascending paralysis, multiple sclerosis, secondary dementia—that sad terminus of the chronic insanities—and many other nervous and mental affections in which the body cell of the neuron—cytoplasm and nucleus—has become destroyed, all belong to the last stages of the pathological process of neuron degeneration, stages which for lack of a better name may be termed *necrotic* neuropathies. The whole pathological process, with its stages and concomitant psychomotor manifestations, may thus be conveniently subdivided into three great classes, one passing into the other by imperceptible degrees: *functional psychosis, functional neuropathy, and necrotic neuropathy.*”

“Now once the neuropathic stages are reached, whether they be the early or the last ones, whether they be the functional neuropathies or the necrotic neuropathies, the functions of the affected neuron-aggregates are gone and lost, temporarily or permanently, according to the stages of the process. In any of the neuropathic stages of the neuropathic process the disturbed, arrested or lost functions are not present in the subconscious. The neuropathies, functional and necrotic, are essentially organic in character. Unlike functional psychosis, the neuropathies have no subconscious ‘equivalents.’ The functions of the neuron-aggregates that have entered the neuropathic stages of the pathological process of neuron degeneration are also lost *subconsciously*. Hence in the neuropathies, even in the early functional stages, no synthesis is possible, because no corresponding subconscious states are present. *The neuropathies have no subconsciousness.*” “*Functional psychosis, functional insanities, should become a special research field of the psychopathologist. Functional psychosis is specially characterized by psychophysiological disaggregation where synthesis is still possible.* The only way of restoring the disturbed equilibrium is to bring about a synthesis of the disaggregated groups with the functioning systems of the upper active personality. Such a synthesis is here brought about by the method of *intermediary* states.”

“The second study, that of alcoholic amnesia, deals with the bringing out of subconscious memories.” “The study coming next in order traces the growth and development of a *persis'ent* dissociated subconscious system and the disturbances brought about by its *periodic eruptions* into the upper strata of mental life. The case with its psychic

manifestations would have ordinarily been classified under the terms of 'psychic epilepsy.'" "The fourth study consists of two parts: the first reviews and discusses phenomena of mental dissociation in an interesting case of depressive delusional states; the second gives experimental data." "The fifth study is on mental dissociation observed in a case presenting limited psychomotor disturbances." "The last study, that of dissociated states in psychomotor epilepsy, deals with the growth and development of a whole system presenting psychomotor disturbances apparently of an epileptic character."

"Throughout the researches the processes both of disintegration and synthesis are followed out. Great stress is laid on *reassociation, or synthesis of dissociated systems and groups in the active personal consciousness*. The processes and modes of synthesis should be closely observed and experimented upon, because they often reveal the character of the constituent elements of the psychic phenomena under investigation, and give an insight into the nature of the synthesized psychic compound. . . . Moreover, if the psychologist and the psychopathologist are interested in the processes of synthesis of disintegrated systems from a purely theoretical standpoint, the physician and the psychiatrist find in the modes and processes of synthesis a very important practical aspect. For from a therapeutic standpoint *synthesis is cure*."

C. J. H.

Treatment of Tabetic Ataxia.¹

One of the draw-backs of anatomical neurology is the satisfaction derived from stereotyped reconstructions of disease-symptoms from the lesions found or suspected and the disregard for those of the usually very variable symptoms which do not fit into the accepted theoretical artefacts. Since the chance for the glory over finding new tracts is diminishing, more credit is again given to unbiased observation of symptoms as such, whether anatomically "explained" or not, and more attention is given to the possible therapeutic utilization of the symptoms as they are.

FRENKEL furnishes a very excellent description of the method of examination of cutaneous, articular, and muscular sensibility, and of the condition of hypotonia, the elements which correct the defects, and their systematic training with detailed description of simple and more complex methods. He uses extensively the finding that the sensibility to active movements is usually much finer than that to passive motion.

On the whole, the sensory features of tabes are mostly used in the explanation, as, indeed, of late years the sensory component of motion has become more and more a necessary and acknowledged certainty.

A. M.

¹The Treatment of Tabetic Ataxia, by means of Systematic Exercise. By H. S. FRENKEL. Translated by L. FREYBERGER. P. Blakiston's Sons. 1902.

Kingsley on the Cranial Nerves of Amphiuma.¹

This study deals primarily with the "topographical relations" of the cranial nerves. It is illustrated with a figure of all the nerves of the head projected upon the frontal plane and with a large and instructive series of drawings of sections in the transverse plane.

The olfactory nerve is found to enter the glomeruli in two roots which are fused peripherally into a common trunk. Of the eye muscles only the oculomotorius was found. It arises, the author states, "from the lower surface of the anterior part of the medulla oblongata." The superior ramus of the nerve innervates the m. r. superior; the distribution of the inferior ramus could not be made out. The author seems to acquiesce unquestioningly in ALLIS' proposition that in the Urodeles the superior branch of the nerve typically innervates the m. r. internus also, and that in this respect the Urodela agree with the Elasmobranchii and Dipnoi rather than with the Anura, Teleostei and Ganoidi. My own researches on *Amblystoma* published in this *Journal* since Professor KINGSLEY's paper appeared, show conclusively that in some Urodeles the superior ramus of the oculomotorius innervates the m. r. superior only, and that in this particular ALLIS' theory can not at present be used with advantage in the solution of taxonomic problems relating to the Amphibia.

The r. mandibularis V. is wholly distinct from the r. maxillaris superior. The motor fibers of the nerve innervate the mm. masseter and temporalis. The sensory component has the distribution usual in Urodela excepting that certain ramuli apparently, not certainly, innervate lateral line sense organs. No anastomosis between this component and the r. alveolaris VII was observed.

A general cutaneous nerve from the Gasserian ganglion fuses with the r. buccalis VII to form the "ramus maxillaris superior." Upon the distribution of these components Professor KINGSLEY contributes important data, i e., that the two branches of the so-called r. maxillaris of *Amphiuma*, which others have described as anastomosing with branches of the r. ophthalmicus profundus, are made up, in part at least, of lateralis VII fibers. The exact nature of these anastomoses is fundamental to a thorough knowledge of the morphology of the r. maxillaris and ophthalmicus profundus, as I have pointed out in my paper on *Amblystoma* (*Jour. Comp. Neurol.* XII, 3, pp. 259, 260).

The ophthalmicus profundus anastomoses by only one branch

¹The Cranial Nerves of *Amphiuma*. By J. S. KINGSLEY. *Tufts' College Studies*, No. 7 (Scientific Series), pp. 293-321.

with the r. palatinus VII. No anastomosis with the olfactorius and no ciliary nerve were found. The root of the auditorius is treated as single. Lateralis motor and communis components are recognized in the facialis roots. The lateralis component goes to form the r. ophthalmicus superficialis, r. buccalis and r. mandibularis facialis externus. That one of the branches of the latter nerve represents the chorda tympani the author is "not disposed to dispute" a position quite inconsistent with the principles of nerve components as it is maintained by other leading neurological morphologists, for the chorda tympani is certainly a visceral sensory nerve. The motor component innervates the digastric and dorso-trachealis muscles. The communis component goes to the r. palatinus, the composition of the r. alveolaris being undetermined. No palatinus caudalis was found.

The author's interpretation of the branchial rami of the glossopharyngeus and vagus seem to me open to some question. In describing the glossopharyngeus (p. 310) he says: "The hyoid division pursues a more direct course forwards and downwards until it reaches the upper surface of the hyoid cartilage along which it courses forwards. It was not traced to the tip. This branch may be the lingualis of authors (which otherwise is not present) . . ." Later (p. 312) he adds: "Just behind the vagus trunk which has just been described, is the branchial trunk of the same nerve. Just after its emergence from the ganglion it gives off, above and in front, a motor branch. . . . The main trunk (*br*¹) is the first branchial nerve. It runs outwards and slightly backwards until it reaches the upper surface of the first epi-branchial, and then turns inwards and forwards along the outer surface of the cartilage. In this as in the other branchial nerves no division was noticed into pre- and post-trematic branches."

"The second third branchial nerves (*br*² and *br*³) leave the ganglion by a common trunk. . . . These pass to the corresponding gill arches much as described for the first branchial."

Now a branch of the glossopharyngeus, such as Professor KINGSLEY describes his "hyoid" branch to be, which enters the hyoid arch, would be considered pre-trematic in fishes; and such a nerve as his "first branchial" would be either a post-trematic of the glossopharyngeus or a pre-trematic of the vagus in fishes. Moreover recent investigations by DRÜNER and myself give abundant evidence that the branchial nerves of many Urodeles divide into pre- and post-trematic rami which hold essentially the same relation to the gill clefts as do the pre- and post-trematic rami of fishes. I venture the proposition, therefore, that Professor KINGSLEY's "hyoid" branch of the glossopharyn-

geus is the r. pre-trematicus IX; and that his first branchial of the vagus is the r. lingualis or post-trematicus of the glossopharyngeus. The fact that Professor KINGSLEY's second and third branchial nerves in *Amphiuma* agree with the first and second branchial trunks of the vagus, as I have described them, in *Amblystoma* (l. c.) in their origin and distribution is additional evidence to support my conclusion.

The r. supratemporalis is recognized as a branch of the glossopharyngeal trunk, and with its description the author gives an instructive comparative discussion. The hypoglossal is formed from the first two spinal nerves, each of which has a dorsal root and ganglion.

G. E. COGHILL.

Regeneration of Peripheral Nerves.¹

FLEMING summarizes the literature on nerve regeneration in the brief statement that there are two theories as to the manner in which peripheral nerves regenerate. (1) The old or central theory, which is that regeneration occurs only from the central end of a divided nerve as a result of the downward growth of central nerve fibers or the axis cylinders of such fibers, in which latter case a new neurilemma is developed from neurilemma nuclei which proliferate during the degeneration of the peripheral segment. This theory FLEMING regards as invalidated by the fact that in a number of cases of secondary nerve-suture, sensation returned, in part at least, in the realm of the sutured nerve in 24 hours, more generally in two to three days; also by a number of more recently recorded observations. (2) The new or peripheral theory, according to which complete degeneration takes place in the peripheral portion of a divided nerve within a period of three to four weeks after section. Within the old neurilemma sheaths, there are developed from the neurilemma nuclei a varying number of cells with large oval nuclei and granular protoplasm, "which, after becoming arranged in more or less regular columns, begin to act as neuroblasts." A wavy axis-cylinder develops close to the nucleus of a young neuroblast, grows and soon becomes separated from the young nucleus by a distinct gap. This young axis-cylinder later becomes invested with a delicate myelin sheath which is either secreted or otherwise developed; the neuroblasts eventually forming the primitive sheath just as in a fully developed nerve fiber. "The new axis-cylinders, while they are joined together to form more or less continuous chains, do not

¹The Peripheral Theory of Nerve Regeneration with Special Reference to Peripheral Neuritis. By R. A. FLEMING, M. A., M. D., F. R. C. P., Ed. *The Scottish Medical and Surgical Journal*. Vol. XI., No. 3, September, 1902.

undergo full development until they are united to the central end of the nerve."

FLEMING, from observations made on *paraffin* sections of nerves stained by the STROEBE method, has convinced himself that the peripheral regeneration theory is correct, although he is not willing to discard entirely the central theory. He describes three of a series of experiments made on rabbits in which the animals were killed 20, 68 105 days after complete section of the nerve. In the first (20 days) there was no evidence of regeneration, in the second and third there was very marked evidence of regeneration in the peripheral segment. Regeneration from the central end was prevented by ligaturing the central end. In his preparations, regeneration in the central end was much more marked than in the peripheral end, "which strongly supports the probability that the central end or old axis-cylinder greatly aids in the process of regeneration." The paper further contains a general statement of the pathologic changes which characterize peripheral neuritis with findings of the appearances presented by the peripheral nerves when stained by the STROEBE method. The reports of the cases given do not admit of abstraction. In certain of the four cases presented and in other cases the study of which was not completed at the time the report was made, peripheral or neuroblastic regeneration was observed, more marked in some of the cases than in others.

The observations recorded in the paper bear evidence of being based on very careful experimental work and on an extended study of autopsy material. It may be permissible, however, to call attention to certain statements made in the above report which need further elucidation before they may be accepted as fully established. The statement is made that as a result of the proliferation of the nuclei of the neurilemma of the degenerating peripheral end of the nerve, young neurilemma cells are formed possessing large oval nuclei and granular protoplasm, "which become arranged in more or less regular columns and begin to act as neuroblasts." Neuroblasts, as is well known, are of ectodermal origin while the neurilemma sheaths with their nuclei are developed from cells of mesenchymal origin (GUKWITSCH). If the peripheral regeneration theory is accepted, we are forced to the conclusion that, while in normal development the neuraxes of neurons are developed from cells of ectodermal origin, during the process of regeneration of peripheral nerve fibers degenerated as a result of section or as a result of changes produced by toxic agents, the neuraxes or axis-cylinders develop from cells of mesenchymal origin, which, after having

performed the function of axis-cylinder formation again assume the role of mesenchymal cells and develop into neurilemmal sheaths. Simple and complex tissues, injured mechanically or by chemic agents, follow, if regeneration ensues, the steps traversed by the respective tissues in their normal development and differentiation. That there should exist such wide departure from this general rule in the case of regenerating nerve fibers seems problematical and can not be conceded without further substantiation.

The majority of investigators who have studied this problem have recognized "the young neurilemma cells," but have not found sufficient evidence to warrant endowing them with neuroblastic function. FLEMING states that the STROEBE method did not give satisfactory results until paraffin sections (which can be cut thinner) were used in place of celloidin sections. It may be stated that HUBER, in an investigation on nerve regeneration published some eight years ago (*Journal of Morphology*, Vol. XI), modified the STROEBE method in the same direction, and in all his experiments saw no evidence of peripheral regeneration. FLEMING further states that an amputation neuroma is not developed solely by neuroblastic formation, "because if a large neuroma is so formed it would necessarily mean that neuroblasts extended so far downward, below what might be called their proper sphere of action, that the neuroblast must be supposed to have almost acquired a malignant tendency and ought to infiltrate muscle and other neighboring tissues." The reviewer finds it still more difficult to explain by the peripheral theory the regeneration of the peripheral portion of a nerve from which a segment measuring 6 to 8 cm. had been removed, the space between the cut ends being bridged by a cat-gut bundle or by a bone tube. In experiments of this kind, naked axis-cylinders were found in the loose connective tissue replacing the absorbed cat-gut or bone tube, and no new axis-cylinders were found in the peripheral portion until the downward growing axis-cylinders developing from the central fibers reached the peripheral end.

Further in regenerating nerve fibers stained by the *intra-vitam* methylen blue method, very fine axis-cylinders are found in the peripheral segment which end at various levels, only a few in the earlier stages of regeneration and a larger number in the later stages. According to the central theory, this fact is readily explained; according to the peripheral neuroblastic theory, an explanation is more difficult. A reason must be given for the fact that certain axis-cylinders in the peripheral segment regenerate and others do not; and also that certain of the regenerating fibers extend further down the peripheral segment than do others.

An acceptance of both theories, as is done by FLEMING, if we read him correctly, is objectionable in that it must be assumed that certain axis-cylinders develop wholly or in part from cells of ectodermal origin, while others in at least a portion of their course develop from cells of mesenchymal origin (neuroblasts developed from neurilemma nuclei).

The early return of sensation in cases of secondary nerve suture is as difficult to explain by the one theory as by the other. The early union of the peripherally developed young axis-cylinders (peripheral theory) with the traumatically injured peripheral ends of the central portion of a nerve after secondary suture does not seem probable and is not born out by experimental proof.

G. C. H.

The Healing of Nerves.¹

This research of BALLANCE and STEWART was undertaken to ascertain the "exact process whereby peripheral nerves, after they have been divided, become reunited," consideration being given to both the degenerative and regenerative processes involved. The observations recorded are based, in the main, on data gained by experimentation on monkeys, dogs, cats and rabbits; material obtained during the operation for secondary nerve suture in man was also studied microscopically and is discussed. The nature of the experimental work was as follows: In certain of the experiments, the nerve was exposed, divided and immediately sutured; in others, a large nerve was divided, the cut ends being left unsutured; in still others, a segment of a nerve was excised, and after periods varying in the different experiments, a portion of nerve sufficient to fill the gap was transplanted. In all, nearly 150 experiments were made. The animals were left after severance of the nerve, for periods varying in the different experiments. The tissues, after fixation in MÜLLER's fluid, or in solutions of formalin, were stained by one of the following four methods:

"1. WEIGERT's method of selective staining of the medullary sheaths.

2. Cox's modification of the GOLGI method for the impregnation of axis cylinders.

3. STROEBE's method for staining of the axis cylinders.

4. VAN GIESON's method for the staining of the cellular and protoplasmic structures."

¹CHARLES A. BALLANCE, M. S., F. R. C. S., and PURVES STEWART, M. A., M. D., M. R. C. P. The Healing of Nerves. Monograph, 112 pp., sixteen plates and one text figure. *Macmillan & Co.*, 1901.

It would be difficult to give even an approximately complete account of the observations made by BALLANCE and STEWART, on the degenerative and regenerative changes observed in severed peripheral nerves, within the limits set for a review, since the greater portion of their monograph consists of a description of the experiments made and of a record of detailed observations made on sections obtained from tissues derived from such experiments. Consideration will, therefore, be given mainly to the deductions made by them, based on a study of their preparations and, in doing so, more particular attention will be paid to their interpretation of the appearances presented by sections showing the regenerative processes in severed peripheral nerves, as their observations can not be said to contribute materially to current views held concerning the degenerative changes occurring in injured peripheral nerves.

In 36 experiments, the severed nerve was removed, sectioned and stained after WEIGERT's differential myelin staining method. In the end of the nerve proximal to the place of section, new sheaths (regenerating nerve fibers) were found as early as the end of the second week. Near the place of division, the new sheaths are said to appear in small isolated groups, "whose general direction is sinuously longitudinal." "At a higher level, adjacent islands of the same longitudinal series have become a continuous tubular plexus within the neurilemma, and higher still the plexus is continuous with the end of the normal sheaths." Particular stress is laid on the fact that in the neighborhood of the wound, the new sheaths appear in the form of isolated groups. The new sheaths are said to be in close opposition to the cells of the neurilemma, which do not share in the degenerative process. Distal to the place of section, new sheaths are visible at the end of the third week and at the end of the following week, they are numerous throughout the entire nerve. In the connective tissue between the distal and proximal segments, the new sheaths are scanty at the end of the fourth week.

Nerve tissues taken from experiments numbering from 38 to 41 were treated after Cox's modification of the GOLGI method. In the preparations showing regeneration, BALLANCE and STEWART observed peculiar cells, impregnated by means of the Cox method, to which they give the name "spider cells." These cells are not especially described, but are abundantly figured on Plates 5 to 12. They appear to consist of a cell body of round or oval shape (somewhat irregular), with numerous processes, which extend generally from opposite poles. The term "spider cell" must be regarded as unfortunate, unless the cells here un-

der consideration are to be regarded as identical with the spider cells (astrocytes) seen in GOLGI preparations of the neuroglia. The spider cells described by these observers are said to be scantily distributed in normal nerves. They are more numerous in regenerating nerves, especially toward the end of the third or fourth week. The processes of these cells are said to run longitudinally and are more numerous and larger in the distal than in the proximal segment and in the intermediate scar tissue the spider cells form an interlacing network. The processes of these cells do not anastomose at this stage in the regeneration of the nerve, though they often overlap. If the reviewer is correct in his interpretation of the account and figures given by BALLANCE and STEWART, the spider cells described by them are to be regarded as the cells from which the new axis cylinders develop.

In experiments numbering from 42 to 84, the nerve tissues were stained by STROEBE'S method for axis-cylinder differentiation. The observations on these preparations corroborate in the main those made on preparations stained after WEIGERT'S differential myelin staining method. Small groups of axis cylinders, stained blue, are seen in the proximal end, "at a considerable distance below the most outlying extremities of the unbroken axis cylinders," by the end of the second week after section. These small bundles or colonies of axis cylinders are said to be found independently of the central axis cylinders. In the distal segment, the regeneration begins somewhat later, also developing, however, as separate threads alongside the elongated nuclei of the neurilemma.

"The new axis cylinders increase steadily in length and in diameter. Their imbricated ends fuse together and at the end of eight weeks, they form long, blue, beaded lines, whose central ends are continuous with the axis cylinders of the proximal segment." These appearances obtain in the distal segment of a divided but sutured nerve. Young axis cylinders were, however, also seen in distal segments not united to the central segments, by the end of the fourth week. These new axis cylinders do not, in unsutured nerves, attain their full maturity; "they show a smaller diameter and are more beaded and sinuous."

In experiments numbering from 86 to 138, the nerve tissues were stained mostly by VAN GIESON'S method, and consideration is given especially to the cellular elements. We shall here, however, consider only their observations on the behavior of the neurilemma nuclei. These nuclei are distinguished from the connective tissue cell nuclei by having an oval shape, while the latter are rod shaped. The neurilemma nuclei begin to proliferate in the distal segment by the end of the sec-

ond day after section, the parent cells dividing in an obliquely longitudinal plane. Mitotic figures are not described nor shown in the plates (Observations of BÜNGER and HUBER). The newly formed neurilemma cells assist in the removal of the "fatty débris of the medullary sheaths and axis cylinders." By the end of the second week, the neurilemma cells develop into elongated cells and these proceed to send out fine protoplasmic processes from the opposite poles, well seen during the fourth and fifth weeks after section; similar appearances are seen in the distal segments of severed nerves not sutured. These elongated cells with polar processes are said to fuse to form the new nerve fibers. In the following brief statement is given a summary of the observations made pertaining to the relation of the neurilemma cells to the newly formed nerve fibers, which may be quoted in full: "The more the specimens are studied the more is the conclusion forced on the mind of the observer that for the regeneration of peripheral nerve fibers (not only the axis cylinders, but also the medullary and neurilemma sheaths) the activity of one variety of cells and of one variety only is responsible. That cell is the neurilemma cell."

BALLANCE and STEWART unhesitatingly declare their adherence to the peripheral theory of nerve regeneration, which is, that the axis-cylinders, medullary and neurilemma sheaths are developed from the neurilemma cells of the degenerated nerve fibers. The processes of regeneration, as observed in the proximal and distal segments of a severed nerve are, according to these observers, essentially the same; the differences observed are "differences of degree and not of kind," since, as has been stated, regeneration of the axis cylinders and medullary sheaths occurs in the distal segment of a severed but unsutured nerve, but the newly formed nerve fibers do not attain their full maturity until they are joined to those of the proximal end. Certain of the conclusions reached by BALLANCE and STEWART seem warranted by the appearances presented by their preparations, which are fully discussed and abundantly figured in this monograph; others, however, appear to me not so well grounded, since the appearances presented by certain of their preparations admit, it is believed, of different interpretations than are given them by these observers; these latter observations may engage our attention primarily. The statement is made that the neurilemma cells of the degenerated portion of the proximal end of a severed nerve assume neuroblastic function and "secrete short segments of axis-cylinders and medullary sheaths," these forming the isolated groups or colonies of newly formed nerve fibers, seen in preparations stained after WEIGERT'S myelin staining method and STROEBE'S

axis cylinder staining method. It seems to me highly probable that these so-called islands or colonies of new axis cylinders, which are said to develop in the more distal end of the proximal segment of a severed nerve, independent of the central axis cylinders, are not such in reality. Observers who adhere to the central theory of regeneration—namely, that the new axis cylinders observed in the degenerated portions of severed nerves in process of regeneration, are outgrowths of the central axis cylinders—have observed small bundles of newly formed axis cylinders or single axis cylinders, which usually present a tortuous course, especially as they approach the region of the wound of the severed nerve. This observation is more explained if we accept BALLANCE and STEWART'S observations on the formation of what they term the "primitive end-bulb," which, as they state, is found within the first and second days after section of the nerve, as a result of "the curling up of the loose ends of the divided fibers." The discursions of these small bundles are of such extent that they are cut several times in sections parallel or nearly so to the long axis of the nerve, and in this manner, as it appears to me, are formed the islands or colonies of newly formed axis cylinders, surrounded by delicate medullary sheaths, described by BALLANCE and STEWART. Carefully made serial sections are necessary to reach correct conclusions on this point. The appearances presented by their preparations do not warrant the conclusions drawn by them (if I may be allowed to interpret their results); these preparations certainly admit of a different interpretation than that which they have given them, and may be used quite as readily to substantiate the central theory of nerve regeneration. In discussing the results which these observers obtained by means of COX'S modification of the GOLGI method, consideration should be given primarily to the method itself. It is of course well known that tissues treated after this method are "stained" by precipitation; cell structures are in no sense differentiated and the relation of fibrillar structures to cell protoplasm is often not clearly and definitely brought out. Attention may be drawn to the results obtained with the GOLGI method in staining neuroglia tissue; in such preparations, the neuroglia fibers are made to appear as processes of the neuroglia cells. The precariousness of the method is such that it must be regarded as somewhat hazardous to make definite statement concerning the length of processes or fibers and of the continuity of fibers, basing such statement on the appearances presented by GOLGI preparations. I can not, therefore, regard the GOLGI method, or modifications thereof, as especially applicable in the study of peripheral nerves in process of degeneration or regeneration. The figures show-

ing results obtained on using the method of Cox, presented by BALLANCE and STEWART, in part at least, appear to reproduce artefacts, since it is more than probable that certain of the processes of the "spider cells," perhaps the greater number of them are in reality fibers which are in close contiguity with the cells or nuclei, which are brought to view by the precipitate and which are included in this precipitate and thus made to appear as cell processes. A comparison may here be drawn between spider cells (astrocytes) and the "spider cells" described by BALLANCE and STEWART; as concerns the former, evidence is at hand which goes to show that certain of the processes of the astrocytes, as seen in GOLGI preparations, are in reality neuroglia fibers which are included in the precipitate which brings to view the cell bodies of the astrocytes, such fibers thus presenting the appearance of processes. Attention may further be drawn to the fact that these observers do not describe and show numerous newly formed medullary sheaths or axis cylinders in relation with one neurilemma cell or nucleus, as might be expected were the processes of the spider cells destined to form new nerve fibers, unless it be assumed that only two of the processes of a spider cell, arising from opposite poles, are concerned in the formation of a new nerve fiber. As previously stated, the use of the term "spider cell" as a means of designating the branched cells seen in peripheral nerves, when stained by the Cox method, as is done by BALLANCE and STEWART, is open to objection, unless it is their desire to imply that these cells present the characteristics of the spider cells (astrocytes) of the central nervous system, in which event it should be recalled that astrocytes (spider cells of the central nervous system—neuroglia cells) are not found in the peripheral nerves (excepting optic and olfactory nerves). In their commentary on the regeneration of axis cylinders stained by the GOLGI method, BALLANCE and STEWART state that "it is clear, then, that the regeneration of axis cylinders does not take place by a process of outgrowth from the proximal segment, but is commenced and completed by the activity of cells already existing in the trunk of the nerve. In the light of what has above been said, it would seem permissible to make use of the Scotch verdict "not proven." The observations of BALLANCE and STEWART pertaining to the regeneration of the peripheral segment of a severed nerve, especially those pertaining to the distal segment of severed but unsutured nerves, are very important and are much more difficult to answer by observers who adhere to the theory of the central origin of newly formed axis-cylinders. BALLANCE and STEWART, as has been stated, find evidence which leads them to say that the new axis cylinders and medullary

sheaths are developed in the peripheral segment from the neurilemma nuclei of the degenerated nerve fibers. They present a text-figure, in which the steps in the differentiation of the neurilemma cells to nerve fibers, as interpreted by them, are clearly shown. It is needless to say that their interpretation of the appearances presented by the distal segment of a severed nerve in process of regeneration is in direct contradiction to the observations made by investigators who have reached the conclusion that regeneration of the peripheral nerves is by a down-growth of central axis cylinders. The writer of the review has observed in his own preparations many of the appearances described by BALLANCE and STEWART, but felt justified in using them in support of the central theory of nerve regeneration, since he never found evidences of regeneration, in the form of newly formed axis cylinders (in preparations stained by the method of STROEBE), until such time as the down-growing axis cylinders reached the peripheral segment. While it is therefore difficult to explain the difference of results obtained and will not be attempted by me, until after renewed investigation of this problem, attention should be drawn to the fact that the observations presented by BALLANCE and STEWART pertaining to the regeneration of the degenerated portion of the central segment of a severed nerve may as readily be used in support of the "central theory" as for the support of the "peripheral theory" of nerve regeneration, as is done by them; and, if used in support of the central theory, for which there is every justification, it is necessary to assume that, while the newly formed axis cylinders of the central segment develop as outgrowths of the central axis cylinders, those of the distal segments are or may be developed from the neurilemma cells, cells of mesenchymal origin, which in embryonic development take no part in the development of the axis cylinders, if we accept the views of the great majority of investigators who have studied the histogenesis of peripheral nerves.

The evidence presented by BALLANCE and STEWART is therefore not sufficient to warrant an overthrow of the views held by the majority of observers who [have investigated] the problem of regeneration of nerve fibers, namely, that the newly formed axis cylinders are outgrowths from the central axis cylinders and that the structural elements of the peripheral segment do not contribute to the axis cylinder formation.

G. CARL HUBER.

Williams on the Embryology and Neurology of the Flat-Fish.¹

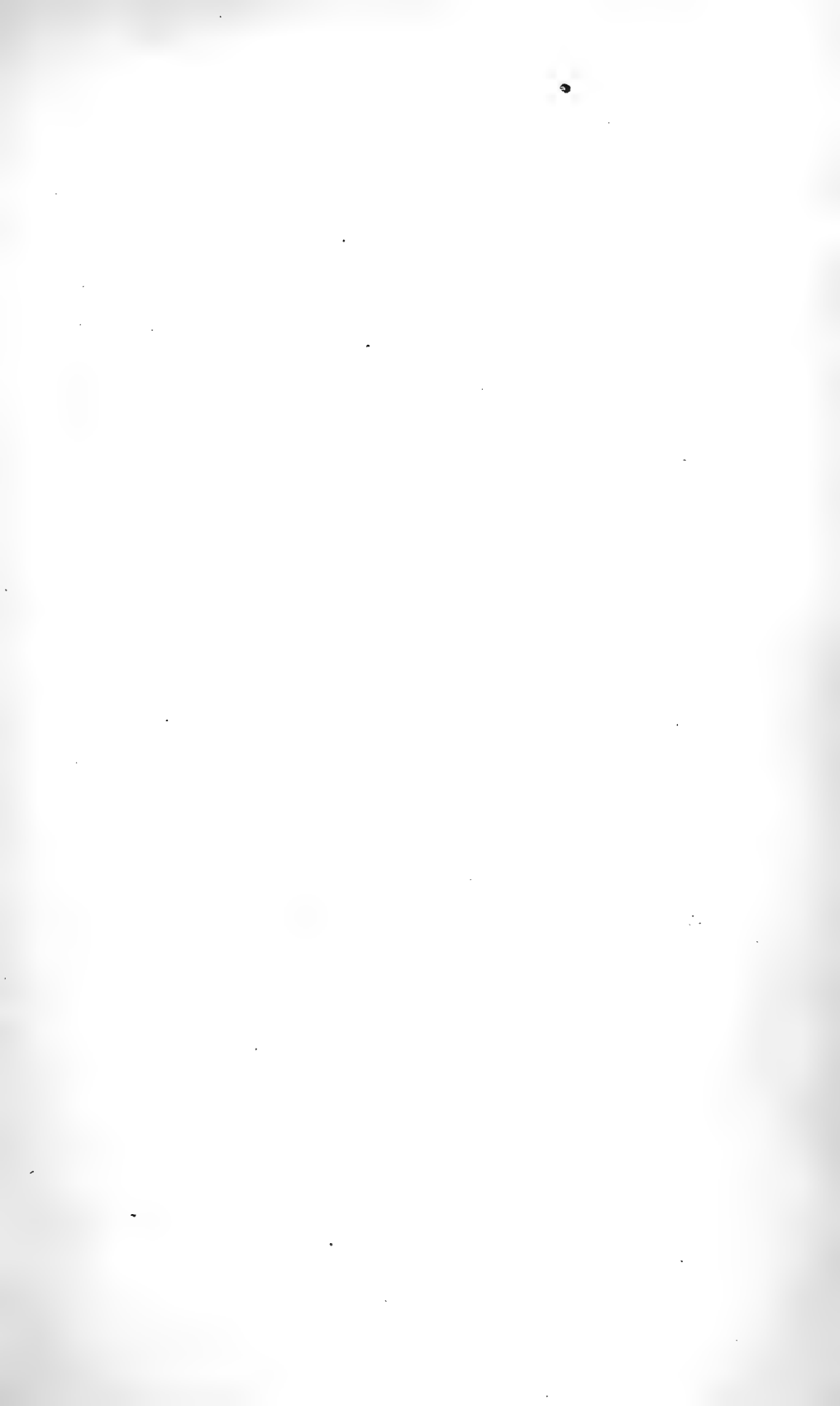
COLE and JOHNSTONE have given us an excellent account of the adult anatomy of a typical flat-fish, and in this research we have a thorough embryological examination of an American representative of the same interesting group. A complete series of embryonic, larval and young forms was studied histologically and the crania of the important stages modeled in wax by BORN's method and reconstructed by the method of projection.

The actual rotation of the eye is very rapid, the greater part of it taking place in not more than three days, though extensive preparations have been made for it in the orbital region for a long time previously. The first observed occurrence in preparation for metamorphosis is the rapid resorption of the part of the supraorbital cartilage bar which lies in the path of the migrating eye. The changes which take place in the head of the flounder in connection with the asymmetry of the eyes all take place in the cartilaginous skull, ossification occurring only after the shifting is complete.

The "optic portion of the central nervous system" is described on pages 23 to 47. A few notes are given on the cranial nerves in general. The optic nerve, optic tracts and tectum opticum are treated more in detail. They present few peculiarities as compared with typical teleosts. Stress is laid on the importance of the nidulus corticalis (of FRITSCH and C. L. HERRICK—Dachkern of EDINGER) as an association center for optic reflexes, confirming the description of C. L. HERRICK. On p. 47 he writes: "The nidulus corticalis, developing early, as it does, is probably one of the most effective association centers of the brain. Lying at the entrance to the tectum, with a strong bundle of neurites running through the two niduli rotundi in the ventral part of the brain, and with its numerous large dendrites passing into layers 3 and 4 of the tectum, it should be able to connect the optic sensory region with the motor areas quickly, and thus account for the extreme rapidity of movement of these larvæ." It appears probable that this nucleus is the same as that described by SARGENT as giving rise to REISSNER's fiber, as intimated by JOHNSTON in his *Acipenser* paper. If so, this adds another important path for optic reflexes from these cells.

C. J. H.

¹WILLIAMS, S. R. Changes Accompanying the Migration of the Eye and Observations on the Tractus Opticus and Tectum Opticum in *Pseudopleuronectes americanus*. *Bul. Mus. Comp. Zool.*, XL, 1, May, 1902.







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